ATTACK, REPRODUCTION, AND DEVELOPMENT OF *IPS CALLIGRAPHUS* (COLEOPTERA: SCOLYTIDAE) IN RELATION TO TEMPERATURE AND SLASH PINE PHLOEM THICKNESS

BY

ROBERT ALLEN HAACK

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

ATTACK, REPRODUCTION, AND DEVELOPMENT OF *IPS CALLIGRAPHUS* (COLEOPTERA: SCOLYTIDAE) IN RELATION TO TEMPERATURE AND SLASH PINE PHLOEM THICKNESS

By

Robert Allen Haack

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Ips calligraphus (Germar) is the major scolytid pest of typical slash pine, *Pinus elliottii* Engelmann var. *elliottii*, the principal crop tree grown in Florida forests. Field reports and rearing experience suggested that *I. calligraphus* infestations and reproductive success were greatest in slash pines with relatively thick phloem (inner bark), but experimental evidence for such a relationship was lacking.

Effects of temperature and slash pine phloem thickness on *I. calligraphus* attack, reproduction, and brood development

were investigated in laboratory and field studies conducted in north-central peninsular Florida. Adult females average 1.8 mm in pronotal width and construct egg galleries primarily in phloem at the phloem-xylem interface. For experimental purposes, "thick" phloem (>beetle width) generally ranged from 2.5-4.0 mm and "thin" phloem (<beetle width) from 0.5-1.5 mm in thickness.

In laboratory studies, female longevity was 66% greater and fecundity 104% greater in thick vs. thin phloem at 30°C. Gallery construction rate and parent-adult residence time were temperature- (positively and negatively correlated, respectively) but not phloem thickness-dependent at 20°, 25°, and 30°C. Reproduction was best in thick phloem at 30°C and poorest in thin phloem at 20°C.

In field studies, I. calligraphus completed 9 generations/year in thick phloem. The distribution of male-constructed nuptial chambers was regular regardless of phloem thickness. Nuptial chambers/dm^2, egg gallery/dm^2, eggs/dm^2, brood/dm^2 and brood survival were all positively correlated with phloem thickness.

In both laboratory and field studies, performance was greater on thick vs. thin phloem considering mean eggs/cm of gallery (38-49% greater), brood adults/parent female (46-107%, laboratory), brood adults/dm^2 of bark (194%, field), and brood adult pronotal width (8% male, 6% female). Time to 50% brood adult emergence occurred 3-4 days sooner on thicker phloem.

Both temperature and phloem thickness were significant factors in the population dynamics of I. calligraphus. This has important implications for rearing, sampling, and population modeling of this bark beetle.

CHAPTER I
INTRODUCTION

Ips calligraphus (Germar) (Coleoptera: Scolytidae) is one of the principal bark beetle pests of pines in the southeastern USA (Wilkinson and Foltz 1980, 1982; Connor and Wilkinson 1983), and of typical slash pine, Pinus elliottii Engelmann var. elliottii, in particular (Fatzinger et al. 1983). In Florida, where slash pine is the most important forest crop tree grown (Sheffield et al. 1983), I. calligraphus has been associated with increased tree mortality in slash pine plantations since 1960 (Chellman 1980).

Two historical points prefacing this study are that (1) laboratory rearing experience indicated that I. calligraphus reproduced best in slash pine logs with relatively thick phloem (inner bark), and (2) in north Florida, I. calligraphus infestations have been greatest in plantations of rapidly growing slash pine trees (G. W. Schlitzkus,[1] personal communication), which typically have thicker phloem. Phloem thickness is known to be a key factor in adult reproduction and brood production of the mountain pine beetle, Dendroctonus ponderosae Hopkins (Coleoptera:

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[1] Forester, Owens-Illinois Inc. Hawthorne, Florida 32640.

Scolytidae), in the western USA (Amman 1972; Amman and Pace 1976; Amman and Cole 1983). The importance of phloem thickness in the population dynamics of the mountain pine beetle is well-recognized as indicated by its inclusion in pest management guidelines (Amman et al. 1977) and risk decision models (Berryman 1982).

The studies described herein were conducted in conjunction with the research program entitled "Sampling and Dynamics of Bark-infesting Beetles in Slash Pine Plantations," which was funded in part by the U.S. Department of Agriculture under the program entitled "The Integrated Pest Management RD&A Program for Bark Beetles of Southern Pines." The specific objective of my research was to investigate I. calligraphus attack, reproduction, and development in relation to temperature and slash pine phloem thickness under both laboratory and experimental field conditions. If temperature and phloem thickness were found to be significant factors in the population dynamics of this bark beetle, the findings could be incorporated into future sampling schemes and pest management guidelines for use in the slash pine ecosystem.

CHAPTER II
GALLERY CONSTRUCTION AND OVIPOSITION BY IPS CALLIGRAPHUS (COLEOPTERA: SCOLYTIDAE) IN RELATION TO TEMPERATURE AND SLASH PINE PHLOEM THICKNESS

Introduction

Bark beetles (Coleoptera: Scolytidae) construct their egg galleries primarily within the phloem (inner bark) tissue of their hosts, at the phloem-xylem interface (Stark 1982). The thickness of the phloem layer, relative to the beetle's size, is important when considering the relative proportions of phloem, xylem, and outer bark through which it tunnels. Since Ips females walk on their tibiae and rotate along their longitudinal axes when tunneling (Schmitz 1972; Gouger et al. 1975), the maximal pronotal width (PW) can be considered one measure of beetle size and serve as an estimate of minimum egg-gallery diameter.

In the relatively large mountain pine beetle (Dendroctonus ponderosae Hopkins; mean PW=2.5 mm, estimated from data in Wood 1982), reproduction was significantly affected by phloem thickness over the range 1.6-4.8 mm in lodgepole pine (Pinus contorta Douglas) (Amman 1972; Amman and Pace 1976). However, for the much smaller southern pine beetle (Dendroctonus frontalis Zimmermann; mean PW=1.2, Wood 1982) no significant relationship was found between its

reproduction and phloem thickness in loblolly pine (Pinus taeda L.) (Wagner et al. 1981a). In that study, phloem thickness generally ranged from 1.1-1.6 mm (T. L. Wagner,[1] personal communication).

Ips calligraphus (Germar) is a major pest of pines in the southeastern USA (Wilkinson and Foltz 1980), and of typical slash pine (Pinus elliottii Engelmann var. elliottii) in particular (Chellman 1980). No studies on the relationship between phloem thickness and I. calligraphus reproductive performance have been reported. This bark beetle is relatively large (mean PW=1.8 mm, Wood 1982), and in slash pine growing in Florida, phloem thickness commonly ranges over 0.5-4.0 mm (unpublished data). Thus a relationship like that between D. ponderosae and P. contorta may exist between I. calligraphus and P. elliottii. The objective of this study was to quantify several measures of I. calligraphus reproduction in relation to slash pine phloem thickness, temperature, and season of year.

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[1] Department of Entomology, Texas A&M University, College Station, Texas 77843.

Methods and Materials

Bark slab preparation. Bark slabs were prepared from 20- to 21-year-old, dominant and co-dominant slash pines growing in a plantation with a site index of 58 ft (17.6 m) at 25 years, near Orange Heights, Alachua County, Florida. Five trees for the fall study and 4 trees for the summer study were felled on 30 September 1981 and 16 June 1982, respectively. The selected trees had phloem thicknesses ranging from 0.5-4.0 mm. After felling, bolts (30-35 cm long) were cut from the trunks between the first and fifth meter, measured from groundline. The bolts were labelled, end-dipped in a benomyl fungicide-water solution (1%), and dried for 3-4 days at 40°C and 40-50% relative humidity (RH). Following drying, loose outer bark flakes were shaved from each bolt, bark at the bolt ends was pared until unstained phloem was detected, bolts were grooved on a table saw, and bark slabs (29-33 cm long, 10-14 cm wide, 2-4 cm thick) were cut away by splitting with ax and hammer. Each slab was coated with paraffin on all cut edges to inhibit contamination and desiccation.

Source of experimental beetles. The parent adults were reared from 2 slash pines, naturally infested subsequent to felling, having ca. 3-mm thick phloem; 1 was felled on 11 September 1981 and the other on 22 May 1982. When most of the developing brood reached the pupal stage, infested trunk

sections were taken to the laboratory and stored in outdoor emergence cages. Emerging brood adults were collected several times daily, sexed according to the form of the third elytral tooth (Hopping 1963), put into containers with moist paper towels, and stored at 20°C until used.

Introduction of beetles into bark slabs. Only mature, non-injured adults that had been collected within 48 h prior to the time of introduction were used. Because Amman (1972) reported a direct relationship between beetle size and both oviposition rate and egg density in D. ponderosae, the few relatively large (PW>2.1 mm) or small (PW<1.5 mm) adults collected were not used. Following the methods of Wilkinson (1964), a "starter hole" (3 mm diam.) was drilled obliquely through the outer bark to the underlying phloem in the center of each slab. A single adult male was placed into the long section of a size 00 gelatin capsule that contained a ring of paper for footing, and that had been pierced on the end for ventilation. The capsule was secured over the starter hole with a ring of Duxseal(R) sealing compound. Males not actively boring within 1 h after introduction were replaced. All males were allowed 24 h to construct a nuptial chamber at 25°C. Three females were then serially introduced in the same manner into each nuptial chamber at 30-45 min intervals. Infested slabs were randomly assigned to one of 3 temperature treatments: 20° (±1), 25° (±1), and 30°C (±1) (photoperiod 12L:12D; 55-70% RH). These

temperatures were selected because in Alachua County, Florida, summer temperatures average near 30°C, while in spring and fall they average near 20°C (Dohrenwend 1978). The infested slabs were held in ventilated rearing cans except for about 30 min daily when radiographed (see below). Each treatment was replicated 18 times in the fall study (162 females) and 20 times in the summer study (180 females).

Data collection. *Ips calligraphus* egg gallery construction, which tends to follow the wood grain (Wilkinson *et al.* 1967), and concomitant oviposition (Gouger !et al.! 1975) were monitored by x-raying the slabs with a Faxitron(R) X-ray unit and Kodak(R) AA film. Each infested slab was radiographed within 1-2 h after introduction of the females and daily thereafter until the egg galleries had been extended to the slab ends. After the last radiograph, the slabs were immediately frozen for 24 h to stop further development and then stored at ca. 4°C in plastic bags. The slabs were later dissected to recover the parent adults and to expose the egg galleries and egg niches located on the sides of the galleries. Recovered parent adults were stored by slab and egg gallery number. An acetate tracing of each slab was made to show the nuptial chamber, egg galleries, and egg niches. The oviposition pattern was reconstructed by identifying the daily increments of egg gallery on the radiographs and marking them on the tracings; egg gallery

was measured in millimeters. In this way, oviposition and gallery construction were recorded for each female, and those values were used to calculate egg density (eggs/cm). The average thickness of the phloem through which each female tunneled was calculated from 3-4 phloem samples taken from the sides of each egg gallery during the dissection process. A dissecting microscope with ocular micrometer was used to measure phloem thickness to the nearest 0.1 mm. The average depth to which each female etched the xylem was calculated from two measurements (nearest 0.05 mm) taken from slab sections cut at right angles to the egg gallery.

Analyses. Data were analyzed by the general linear models procedures of the Statistical Analysis System (SAS), version 1979.6. Analyses were based on the first 4 days of egg gallery construction at 30°, first 6 days at 25°, and first 8 days at 20°C -- the times when most females were in close proximity to the slab ends at each temperature. Only those females that remained alive and constructed gallery throughout the study were included (171 in summer; 138 in fall). Mean sizes of parent adults, as determined by elytral length (measured dorsally) and pronotal width (measured dorsally at the widest point), was compared both within and between studies with the Duncan's multiple-range test. Regressions of oviposition rate (OR, eggs/day), gallery construction rate (GCR, cm/day), length of initial egg-free gallery (PRE-EG, mm), egg density (ED, eggs/cm),

and depth of xylem-etching (DXE, mm) were each performed over the entire data set, with phloem thickness (PT) as the independent variable and season (S) and temperature (T) as class variables. Significance of all main effects and interactions was tested at the $P<0.05$ level. PRE-EG was determined by measuring the length of gallery from where each female began tunneling (as determined from the first radiograph) to her first egg. Linear regression of ED with PT was performed after log-log transformation of the data (Steel and Torrie 1980), because of the curvilinear relation observed between these 2 variables. Egg density was defined as follows:

ED = total eggs / (total gallery length - PRE-EG).

Results

Beetle size. Mean adult size for each sex did not differ significantly ($P>0.05$) between studies, nor among temperature treatments within each study. Therefore, beetle size is not considered a factor in the response variable differences noted below. For all recovered adults, mean pronotal width and elytral length were 1.80 mm (±0.09 SD) and 2.52 (±0.13) for males (N=100), and 1.71 (±0.08) and 2.50 (±0.12) for females (N=296), respectively. The relationship between pronotal width (PW, mm) and elytral length (EL, mm) by sex was PW = 0.531 + 0.503 EL ($r^2=0.527$, Sy.x=0.048, N=100) for males, and PW = 0.419 + 0.515 EL ($r^2=0.528$, Sy.x=0.028, N=296) for females.

Oviposition rate (OR). The number of eggs laid per female per day was significantly related to season, temperature, phloem thickness and 3 interactions between these factors (Table 2-1). Temperature and phloem thickness were the principal factors influencing OR. Oviposition rate was positively correlated with temperature and phloem thickness in both summer and fall (Fig. 2.1). Extremes of individual oviposition rates ranged from 1.1 eggs/day (20°C, PT=0.8 mm) to 20.3 (30°C, 3.5 mm) in the fall study, and from 1.1 (20°C, 0.6 mm) to 19.3 (30°C, 3.6 mm) in the summer study.

Gallery construction rate (GCR). The length of gallery constructed per female per day was significantly correlated with season, temperature, phloem thickness, and 3 interactions between these factors (Table 2-1). Temperature was the major factor affecting GCR; the 2 were positively correlated. Mean GCR was 1.67 cm/day (±0.36) at 20° (N=96), 2.41 (±0.37) at 25° (N=108), and 3.34 (±0.73) at 30°C (N=105). Because of the weak association of GCR with PT (r^2=0.014) predictive equations incorporating phloem thickness were not considered. When the data sets for each study were analyzed independently, GCR was significantly ($P<0.05$) related to PT in the fall study only. Extremes of individual gallery construction rates ranged from 0.9 cm/day (20°C, PT=0.7 mm) to 5.7 (30°C, 3.5 mm) in the fall study, and from 1.0 (20°C, 3.0 mm) to 4.9 (30°C, 2.6 mm) in the summer study.

Initial egg-free gallery (PRE-EG). The amount of gallery between the nuptial chamber and the first egg was significantly associated with season, temperature, and phloem thickness (Table 2-1). Temperature was the principal factor influencing PRE-EG; the 2 were negatively correlated. Because PT explained only 1.7% of the model variation, predictive equations incorporating phloem thickness were not considered. Again, when the data sets for each study were analyzed independently, PRE-EG was significantly ($P<0.05$) related to PT in the fall study only. Mean distance to the first egg was significantly ($P<0.05$) shorter in the summer study than in the fall study at 25° and 30° but not at 20° (Table 2-2). Also, mean distance to the first egg tended to shorten with increasing temperature in both studies. Extremes of individual egg-free gallery lengths ranged from 6 mm (30°C, PT=0.6 mm) to 57 (25°C, 1.0 mm) in the fall study, and from 7 (30°C, 1.5 mm) to 49 (20°C, 2.5 mm) in the summer study.

Egg density (ED). The number of eggs laid per unit length of gallery was significantly related to phloem thickness, temperature, season, and 1 interaction term (Table 2-1). Phloem thickness was the major factor explaining the observed variation in ED. Egg density was positively correlated with phloem thickness and temperature in both the summer and fall studies (Fig. 2-2). Extremes of individual egg densities ranged from 1.1 eggs/cm (20°C,

PT=0.8 mm) to 5.1 (30°C, 3.4 mm) in the fall study, and from 1.3 (20°C, 0.6 mm) to 11.0 (30°C, 3.5 mm) in the summer study.

Depth of xylem-etching (DXE). The depth to which females etched the xylem was significantly associated with season, temperature, and phloem thickness (Table 2-1). Phloem thickness was the principal factor affecting DXE; the 2 were negatively correlated. Females tended to etch more xylem than outer bark until phloem became less than ca. 0.8-mm thick, after which more outer bark was etched. Egg gallery diameters and female pronotal widths ranged from 1.7-2.1 mm and 1.5-1.9 mm, respectively. The overall regression equation for DXE (mm) with PT (mm) was DXE = 0.503 - 0.119 PT (r^2=0.656, Sy.x=0.009, N=309). Extremes of individual depths of xylem etching ranged from 0.7 mm (30°C, PT=0.8 mm) to 0.05 (30°C, 3.5 mm) in the fall study, and from 0.7 (20°, 0.7 mm) to 0.05 (30°, 3.3 mm) in the summer study.

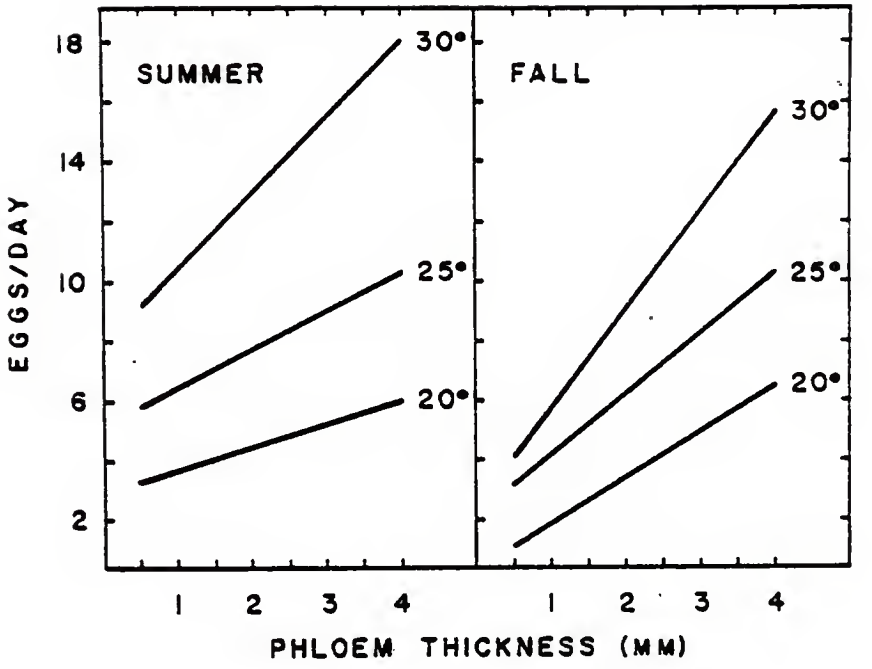

Fig. 2-1. Ips calligraphus oviposition rate (OR; eggs/day) at 3 temperatures in bark slabs from slash pines cut in fall (F) 1981 and summer (S) 1982, and having phloem thicknesses ranging from 0.5-4.0 mm. Equations were based on first 8 days of oviposition at 20°, first 6 days at 25°, and first 4 days at 30°C, beginning at time of female introduction (overall r^2=0.86; overall Sy.x=0.24; N=309). Individual equations of OR with PT are:

S,30° (N=59) OR=7.88+2.54 PT	F,30° (N=46) OR=2.50+3.30 PT
S,25° (N=59) OR=5.16+1.28 PT	F,25° (N=49) OR=2.17+2.04 PT
S,20° (N=53) OR=2.87+0.78 PT	F,20° (N=43) OR=0.39+1.54 PT

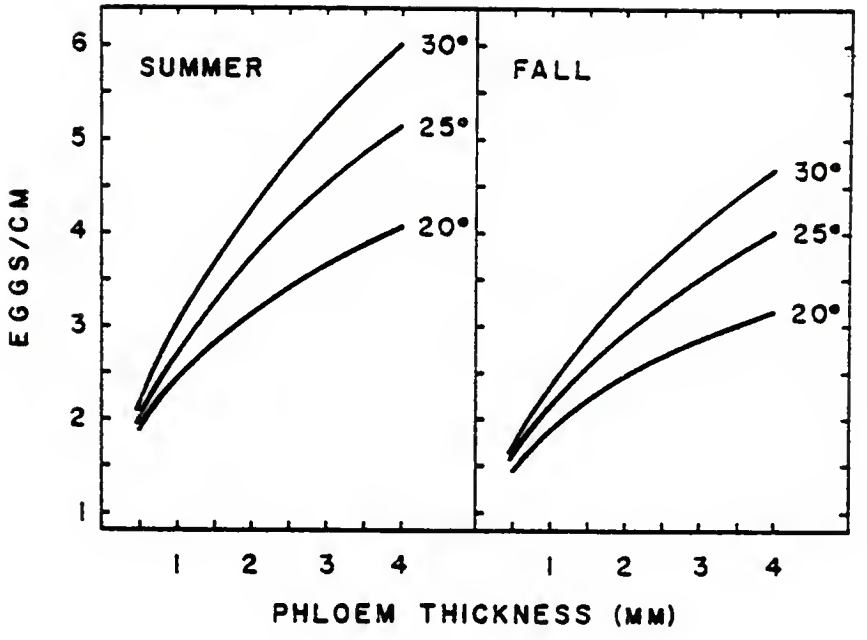

Fig. 2-2. Ips calligraphus egg density (ED; eggs/cm) at 3 temperatures in bark slabs from slash pines cut in fall (F) 1981 and summer (S) 1982, and having phloem thicknesses ranging from 0.5-4.0 mm. Equations were based on first 8 days of oviposition at 20°, first 6 days at 25°, and first 4 days at 30°C, beginning at the first egg (overall r^2=0.73; overall Sy.x=0.05; N=309). Individual equations of ED with PT are:

S,30°(N=59)	$ED=3.01\ PT^{0.50}$	F,30°(N=46)	$ED=2.34\ PT^{0.50}$
S,25°(N=59)	$ED=2.76\ PT^{0.45}$	F,25°(N=49)	$ED=2.15\ PT^{0.45}$
S,20°(N=53)	$ED=2.44\ PT^{0.32}$	F,20°(N=43)	$ED=1.90\ PT^{0.32}$

Table 2-1. Partial and overall coefficients of determination (r^2) and their corresponding significance levels for linear regression model variables pertaining to Ips calligraphus oviposition rate (OR), gallery construction rate (GCR), initial egg-free gallery (PRE-EG), egg density (ED), and depth of xylem-etching (DXE), at 20°, 25°, and 30°C in slash pine bark slabs prepared during the fall (1981) and summer (1982) seasons. Regression was performed using phloem thickness (PT) as the independent variable and with season (S) and temperature (T) as class variables.

Model Variable	Oviposition and Gallery Parameters				
	OR	GCR	PRE-EG	ED[1]	DXE
S	0.090**[2]	0.007*	0.050**	0.179**	0.011**
T	0.536**	0.631**	0.212**	0.152**	0.031**
PT	0.179**	0.014**	0.017**	0.397**	0.622**
SxT	0.022**	0.015**	n.s.	n.s.	n.s.
SxPT	0.008**	0.046**	n.s	n.s.	n.s.
TxPT	0.025**	n.s.	n.s.	0.006*	n.s.
SxTxPT	n.s.	0.023**	n.s.	n.s.	n.s.
Overall	0.860**	0.736**	0.279**	0.734**	0.664**
N	309	309	309	309	309

[1]Linear regression of ED with PT was performed after log-log transformation of the data.

[2]n.s. = not significant at the $P<0.05$ level, * = $P<0.05$, ** = $P<0.01$.

Table 2-2. Length (mm) of Ips calligraphus initial egg-free gallery (PRE-EG) at 20°, 25°, and 30°C in slash pine bark slabs that were prepared during the fall (1981) and summer (1982) seasons.

	Initial Egg-free Gallery Length (mm)		
	20°	25°	30°
Season	$\bar{X} \pm SD$ (N)	$\bar{X} \pm SD$ (N)	$\bar{X} \pm SD$ (N)
Fall	24.2±7.7 a1[2] (43)	21.4±7.3 a1 (49)	17.7±6.1 a2 (46)
Summer	23.3±7.6 a1 (53)	17.1±5.0 b2 (59)	13.5±3.4 b3 (59)

[1]Initial egg-free gallery was measured from the point where each female began tunneling to her first egg.

[2]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

Discussion

Several investigators have attributed observed variations in beetle reproduction to changes in the quality of the beetles themselves (Sahota and Thomson 1979; Wagner et al. 1981a). However, it may be changes in host quality that offer the principal explanation for the variations noted in this study. Ips calligraphus adults are liquid-feeders, obtaining nutrients from the tissues through which they tunnel (Gouger et al. 1975). Thus, the observed variations in I. calligraphus reproductive performance are probably related to the following points.

1. Physical and nutritional differences that exist among xylem, phloem, and outer bark.
2. Seasonal changes that occur within these plant tissues.
3. Differences in the relative proportions of these tissues that are encountered when tunneling in thin versus thick phloem.

The xylem in pines consists of mostly thick-walled, highly lignified cells. The outer bark contains weakly lignified, heavily suberized cells (suberin is a waxy substance), and the phloem is mostly thin-walled, unlignified and unsuberized cells (Howard 1971; Koch 1972). Water content is usually higher in phloem than in either xylem or outer bark, average values for slash pine being 69% (Martin 1969), 47% (Miller 1959), and 20% (Martin 1969),

respectively. In trees, water content is generally inversely related to specific gravity, a measure of density (Koch 1972). Seasonal changes are especially apparent in xylem. In slash pine, the relatively thick-walled latewood cells (nearest the phloem in the fall study) are 2-2.5 times more dense than are earlywood cells (nearest the phloem in the summer study) (Paul 1939; Ifju 1969). Thus, in conducting xylem, water content would apparently be lower in latewood than in earlywood. Also, the nutritional qualities of xylem, phloem, and outer bark are quite different. Concentrations of carbohydrates, lipids, and nitrogenous compounds are generally highest in phloem, lower in xylem, and lowest in outer bark (Kramer and Kozlowski 1979).

Considering these known differences in the tissues of pines, tunneling in thin phloem most likely requires additional energy because more of the adjacent xylem and outer bark is etched. Furthermore, more energy is probably expended when etching latewood as opposed to earlywood xylem. Similarly, females would apparently obtain fewer nutrients per unit length of gallery when tunneling in thin phloem. Consequently, the resources necessary for egg production are obtained over longer distances in thinner phloem, and thus, OR and ED tend to be lower in thinner phloem. The overall greater reproductive performance by females in the summer study may, in part, reflect the relatively lower density and higher moisture content of

earlywood versus latewood xylem. The greater egg densities at the higher temperatures shown in Fig. 2-2 may indicate increased efficiencies of conversion and assimilation of ingested food with increasing temperature (Sahota and Thomson 1979; Scriber and Slansky 1981).

As was the case in our study, Amman (1972) reported no strong correlation between phloem thickness and gallery construction rate. A plausible explanation is that per cm of gallery, females in thin phloem must spend relatively more time tunneling than ovipositing, whereas females in thick phloem spend more time ovipositing than tunneling. As a result, gallery construction rate is similar over a wide range of phloem thicknesses.

The inverse relationship between I. calligraphus initial egg-free gallery and temperature (Table 2-2) is similar to that reported for several species of Dendroctonus (Sahota and Thomson 1979; Wagner et al. 1981a). This relationship probably reflects temperature-dependent processes that occur in the flight muscles, fat body, reproductive organs, and corpora allata (Reid 1958; Atkins and Farris 1962; Sahota and Thomson 1979). Shorter distances to first oviposition in the summer study at 25° and 30°C may reflect the density and moisture differences between earlywood and latewood.

The fact that I. calligraphus oviposition rate and egg density were positively correlated with phloem thickness indicates that great care should be taken when selecting

host materials for biological studies of bark beetles. This would be especially important when using tree species with phloem thicknesses that bracket the range of adult sizes found in the beetles under study. Phloem thickness and reproduction may not have correlated in the southern pine beetle study (Wagner et al. 1981a) because the phloem was generally thick relative to beetle width. In contrast, in the mountain pine beetle studies (Amman 1972; Amman and Pace 1976) and in our own work, where there are significant changes, phloem thickness has ranged from thinner to thicker than beetle width.

Summary

In summary, the following points can be made with respect to I. calligraphus gallery construction and reproduction in relation to phloem thickness and temperature.

1. Gallery construction rate is positively correlated with temperature, but apparently little affected by phloem thickness.
2. Females etch deeper into the xylem as phloem becomes thinner. Temperature has no apparent effect on depth of xylem etching.
3. Oviposition rate and egg density (eggs/cm of gallery) are positively correlated with both phloem thickness and temperature. These measures of reproductive performance were greatest with a combination of

thicker phloem (3-4 mm) and warmer temperature (30°C).

4. The length of gallery that females construct before first oviposition is negatively correlated with temperature, and apparently unaffected by phloem thickness.
5. Under similar conditions of phloem thickness and temperature, reproductive performance is greater when earlywood is outermost in the current annual ring of xylem (this was the case in the summer study) than when latewood is outermost (fall study). Such a finding demonstrates that seasonal variations in host materials should be considered in biological studies of phloem-dwelling insects, especially for multivoltine species.
6. The above results indicate that phloem thickness should be considered in population dynamics studies of I. calligraphuus in slash pine, especially in summer when warmer temperatures accentuate phloem thickness effects on female reproduction.

CHAPTER III
LONGEVITY AND FECUNDITY OF IPS CALLIGRAPHUS (COLEOPTERA: SCOLYTIDAE) IN RELATION TO SLASH PINE PHLOEM THICKNESS

Introduction

Bark beetles (Coleoptera: Scolytidae) tunnel and oviposit primarily in the phloem (inner bark) tissue at the bark-wood interface of the host tree (Stark 1982). Actual values of bark beetle fecundity are difficult to obtain because parent adults commonly re-emerge after establishment of their first brood and go on to construct another egg gallery elsewhere (Coulson *et al.* 1978). Thus, only a fraction of a female's eggs are deposited in any one gallery. Nevertheless, estimates do exist for a few species of bark beetles. Under natural conditions, Reid (1962) found 263 eggs in a single gallery of *Dendroctonus ponderosae*. In laboratory studies terminated after 30 days, mean fecundity was 159 eggs for *Dendroctonus frontalis* at 28°C (Clarke *et al.* 1979); and similarly, using females reared from natural populations, 77 for *Ips avulsus* (Eichhoff), 117 for *Ips calligraphus*, and 108 for *Ips grandicollis* (Eichhoff) at 30°C (Yearian *et al.* 1972). In a different study, at various temperatures, maximum fecundity during a 30-day period was 109 for *I. avulsus*, 274 for *I. calligraphus*, and 206 for *I. grandicollis* (Dale 1967).

While constructing an egg gallery, females obtain liquid nourishment from the host tissues through which they tunnel (Gouger et al. 1975). The thickness of the phloem layer with respect to the beetle's size affects the relative proportions of xylem, phloem, and outer bark encountered while tunneling. Amman (1972) reported that D. ponderosae etched deeper into xylem as phloem became thinner, and that oviposition rate (eggs/day) and egg density (eggs/cm of gallery) were significantly lower in thinner phloem. I reported similar correlations for I. calligraphus in typical slash pine, Pinus elliottii, in chapter II. In that study, phloem thickness effects on I. calligraphus oviposition rate and egg density were greatest at 30°C (see Figs. 2-1 and 2-2). However, at that temperature, oviposition was monitored for only a 4-day period. Thus, the effects of phloem thickness on overall female longevity and fecundity were not observed. The objective of this study was to record I. calligraphus longevity and fecundity at 30°C in relation to slash pine phloem thickness.

Methods and Materials

Bolt preparation. Rearing bolts (35 cm long) were prepared from 21-year-old slash pine trees growing in a plantation with a site index of 58 ft (17.6 m) at 25 years, near Orange Heights, Alachua County, Florida. Fifteen trees were felled between 12 April and 16 June 1982 to ensure

having adequate numbers of rearing bolts available. Phloem thickness at breast height (1.4 m) measured 1.0-1.5 mm on 7 of these trees, and 2.5-3.5 mm on the other 8. These ranges of phloem thickness were considered, respectively, "thin" and "thick" relative to the size of I. calligraphus adults from Florida (about 1.5-2.1 mm, see chapter II). After felling, bolts were cut from the 2- to 6-m section of the trunk, measured from groundline. The bolts were labelled and dried for 3-4 days at 40°C and 40-50% RH. Following drying, the loose outer bark was removed and the bolt ends were pared back to unstained phloem. The bolt ends were then dipped in a benomyl fungicide-water solution (1%) and melted paraffin to inhibit contamination and desiccation. The bolts were stored at 20°C until used.

Source of experimental beetles. The beetles used to initiate the study were reared from a 21-year-old slash pine tree with thick phloem that was naturally infested subsequent to felling on 19 March 1982. When most of the developing brood reached the pupal stage, infested sections of trunk were returned to the laboratory and stored in screen emergence-cages in an open-air insectary. Emerging brood adults were collected several times daily, sexed according to the form of the third elytral tooth (Hopping 1963), put into containers with moist, brown paper towels, and stored at 20°C until used. To ensure a sufficient number of males throughout the study, 2 additional pines

with thick phloem were felled and treated as above; felling dates were 23 April and 22 May 1982.

Introduction and transfer of beetles. Only females collected within 24 h, and males within 48 h, prior to the time of introduction were used as parent adults. Following the methods of Wilkinson (1964), "starter holes" were made through the outer bark along the bolt mid-line. From 2-6 starter holes were made per bolt with no 2 holes closer than 10 cm. A single adult male was placed into the long section of a size 00 gelatin capsule that contained a ring of paper for footing, and that had been pierced at the end for ventilation. The capsule was placed over the starter hole and held there with a ring of Duxseal(R) sealing compound. Males were allowed 24 h at 30°C to construct their nuptial chambers, after which time 1 female was introduced into each chamber in similar fashion. A code number for each female was written on the outer bark next to the nuptial chamber she had entered. These bolts were placed into ventilated rearing cans and maintained at 30°C, 60-70% RH, and photoperiod 12L:12D. Three days later, each gallery system was dissected and the female removed and immediately introduced into another nuptial chamber on a different bolt. This period of time was chosen because after 3 days of tunneling, females would be nearing either the top or bottom of the bolt. These "new" nuptial chambers had been constructed over the previous 24 h by recently emerged

males. In general, males were used to construct only a single nuptial chamber, after which they were frozen. In this manner, 40 females were transferred from one set of males and bolts to another every 3 days until all females had died. There were 4 treatments (N=10 each) with respect to female transfer:

1. From thick phloem to thick phloem only (KK).
2. Alternating between thick and thin phloem, beginning on thick (KN).
3. Alternating between thick and thin phloem, beginning on thin (NK).
4. From thin phloem to thin phloem only (NN).

Data collection. Each female's ovipositional history was recorded by making acetate tracings of all the egg galleries that she made during her lifetime. Each tracing included the nuptial chamber, the entire egg gallery, and the location of all egg niches. Total number of eggs, total gallery length (measured in mm beginning at the first egg), and longevity (days) were recorded for each female. Using the above values, egg density (eggs/cm of gallery), oviposition rate (eggs/day), and gallery construction rate (mm/day) were recorded. Additionally, for those females switched between thick and thin phloem, numbers of eggs laid in the first (beginning at the first egg) and last 2 cm of each gallery were recorded.

For several females the exact day on which death occurred was not certain. In such cases, the day was estimated by comparing the length of that individual's final gallery to the one she had constructed the previous 3 days, and by comparing the developmental stage of her last eggs (if any) to those of females that lived and oviposited the entire 3-day period.

Because a direct relationship between female size and reproductive performance has been reported for other bark beetles (Reid 1962; Amman 1972; Clarke et al. 1979), mean size of the females used in this study was analyzed among treatments. The maximal pronotal width was used as an indicator of female size; it was measured dorsally to the nearest 0.05 mm using a dissecting microscope with ocular micrometer.

The average thickness of phloem through which each female had tunneled was calculated from 2-3 samples taken less than 1 cm from the sides of her egg gallery during bolt dissection; samples were removed with a knife. Phloem thickness was measured to the nearest 0.1 mm. The phloem water content of each bolt was also calculated from 4-6 samples taken no less than 5 cm from an egg gallery during bolt dissection. After removal, samples were immediately weighed in milligrams, dried to no further weight change (ca. 3 days) at 55°C, and reweighed. Percent water content (PWC) was recorded on a wet-weight basis:

$$PWC = 100 \times (\text{Fresh wt} - \text{Dry wt}) / \text{Fresh wt}.$$

Analyses. Data were analyzed with the t-test and general linear models procedures of the Statistical Analysis System (SAS), version 1982.3. Preliminary analyses, using the t-test, indicated no significant differences ($P>0.05$) between the KN and NK treatments as measured by mean longevity ($P>0.90$), mean total gallery length ($P>0.75$), and mean fecundity ($P>0.73$). Data from these 2 treatments were thus pooled in all subsequent analyses, except where indicated below.

Mean female prothoracic width, longevity, total gallery length (TGL), gallery construction rate (GCR), fecundity, oviposition rate (OR), and egg density (ED) were compared among the 3 treatments (KK, KN+NK, NN) using Duncan's multiple-range test. Additionally, mean TGL, fecundity, and ED were compared by means of analysis of covariance using "age" (i.e., longevity) as the covariate. Similarly, mean GCR, OR, and ED were compared both within and among the 4 original treatments (KK, KN, NK, NN) for each 3-day oviposition period. Regression analyses of longevity, TGL, GCR, fecundity, OR, and ED were each performed separately with female prothoracic width, after sorting by treatment. Similarly, regressions were performed on female survival (number alive at end of each 3-day period), GCR, OR, and ED, using female age as the independent variable; data from each 3-day oviposition period were used in these analyses. For those females switched between thick and thin phloem (KN and

NK), t-tests were used to compare (1) overall GCR, OR, and ED while in thick phloem to that while in thin phloem, and (2) ED over the first 2 cm of egg gallery to that over the last 2 cm. In the latter analysis, only data from the 2nd-7th gallery (days 4-21) were used. Mean percent water content was compared between thick- and thin-phloem bolts by the t-test without transformation.

Results

Female size. Mean pronotal width of the parent females did not differ significantly ($P>0.97$) among the 3 treatments (KK, KN+NK, NN). Female size was thus not considered to be a significant factor in the response variable differences noted in the subsequent among-treatment comparisons. Mean pronotal width was 1.77 mm ($\pm$0.09 SD) for the 40 females, and 1.84 ($\pm$0.10) for a sample (N=50) of the 321 males used throughout the study. Pronotal widths ranged from 1.6-1.95 mm for females and from 1.7-2.1 for males.

Longevity. Females lived significantly ($P<0.05$) longer on KK than on NN (Table 3-1), averaging 66% longer on KK. No significant linear relationship was found between longevity and female pronotal width within any of the 3 treatments ($P>0.82$ KK; 0.56 KN+NK; 0.72 NN). The numbers of females alive at the end of each 3-day oviposition period are presented in Table 3-2 by treatment; the values given in

Table 3-2 are the "N" values for Tables 3-4 to 3-6. Equations based on regression analyses of female survivorship with female age are presented in Table 3-3. Survival curves fo the treatments KK, KN+NK, and NN are shown in Fig. 3-1.

Total gallery length (TGL). The total length of all galleries constructed per female lifetime did not differ significantly ($P>0.10$) among treatments (Table 3-1). Similar results were obtained when mean TGL was compared among treatments using female age as covariate. No significant linear relationship was found between TGL and female pronotal width within any of the 3 treatments ($P>0.81$ KK; 0.27 KN+NK; 0.42 NN).

Gallery construction rate (GCR). Females constructed significantly ($P<0.05$) more gallery per day on KN+NK than on KK (Table 3-1), averaging 24% more on KN+NK. Only in the NN treatment was there a weakly significant ($P<0.07$ NN; >0.71 KK; >0.96 KN+NK) correlation between GCR and female pronotal width (PW; mm): GCR = 79.9 - 26.8 PW ($r^2=0.34$; N=10). Mean GCR values for each 3-day period are compared both within and among treatments in Table 3-4. In general, GCR decreased with female age; no distinct differences were noted among treatments. Equations based on regression analyses of GCR with female age are presented in Table 3-3; in all treatments, a negative correlation exists between

these two variables. In a combined regression analysis, using treatment as a class variable, both treatment and age added significantly ($P<0.01$ for both) to the overall equation; treatment accounted for 5% of the total variation and age 46% (overall $r^2=0.51$; N=311). For females switched between thick and thin phloem, mean GCR while on thick phloem did not differ significantly ($P>0.19$) from that while on thin phloem; mean values were 30.6 mm/day ($\pm$10.9, N=75 galleries) and 33.8 ($\pm$12.4, N=76), respectively.

Realized fecundity. The total number of eggs laid per female lifetime was significantly ($P<0.05$) greater on KK than on NN (Table 3-1), averaging 104% more on KK. Similar results were obtained from the analysis of covariance using female age as covariate. No significant linear relationship was found between fecundity and female pronotal width within any of the 3 treatments ($P>0.80$ KK; 0.34 KN+NK; 0.55 NN).

Oviposition rate (OR). Females laid significantly ($P<0.05$) more eggs per day on KK than on NN (Table 3-1), averaging 27% more on KK. No significant linear relationship was found between OR and female pronotal width for any of the 3 treatments ($P>0.42$ KK; 0.79 KN+NK; 0.27 NN). Mean OR values for each 3-day period are compared both within and among treatments in Table 3-5. OR was generally greater on thick phloem (KK) than on thin phloem (NN) during days 6-15. Overall, OR decreased with age within each

treatment; regression equations of OR with female age are presented in Table 3-3. The relatively low coefficient of determination for the KN+NK treatment (r^2=0.28) probably reflects how OR fluctuated as a result of the females being switched between thick and thin phloem. In a combined regression analysis, using treatment as a class variable, both treatment and age added significantly (P<0.01 for both) to the equation; treatment accounted for 3% of the total variance and age 41% (overall r^2=0.44; N=311). For those females alternating between thick and thin phloem, mean OR on thick phloem was significantly (P<0.01) greater than that on thin phloem; mean values were 13.2 (±5.2, N=75 galleries) and 10.0 (±5.1, N=76), respectively.

Egg density (ED). Females laid significantly (P<0.01) more eggs per cm of gallery on KK than on NN (Table 3-1), averaging 49% more on KK. Similarly, ED averaged 25% greater on KN+NK than on NN. A similar ranking of the means was determined from an analysis of covariance using female age as covariate. No significant linear relationship was found between ED and female pronotal width for any of the 3 treatments (P>0.53 KK; 0.73 KN+NK; 0.69 NN). Mean ED values for each 3-day period are compared both within and among treatments in Table 3-6. In general, ED tended to decline with female age in all treatments; equations based on regression analyses of ED with female age are presented in Table 3-3. Overall, ED was consistently greater for females

in thick phloem (KK) than in thin phloem (NN) over the first 21 days of oviposition. In the combined regression analysis, using treatment as a class variable, both treatment and female age added significantly ($P<0.01$ for both) to the overall equation; treatment accounted for 8% of the total variance and age 11% (overall $r^2=0.19$; N=311).

The density of eggs laid by females repeatedly switched between thick and thin phloem generally increased while on thick phloem and decreased on thin phloem (Fig. 3-2). Overall, ED was 4.3 (±1.2, N=75 galleries) eggs/cm on thick phloem, and 2.8 (±1.1, N=76) on thin phloem. More specifically, ED changed significantly ($P<0.01$) between the beginning and end of the galleries. Females switched from thin into thick phloem produced 3.8 (±1.1) eggs/cm in the first 2 cm and 5.0 (±1.3) in the last 2 cm (N=46 galleries). Females switched into thin phloem had egg densities decline from 3.5 (±1.1) at the beginning of the gallery to 2.4 (±1.5) at the end (N=49).

Phloem water content (PWC). Average phloem water content (%) did not differ significantly ($P>0.83$) between the 2 phloem thickness classes. Mean PWC was 68.6% (±4.3, N=40 bolts) for thick phloem, and 68.4% (±3.4, N=44 bolts). For individual bolts, PWC ranged from 60-76% in thick phloem, and from 60-74% in thin phloem.

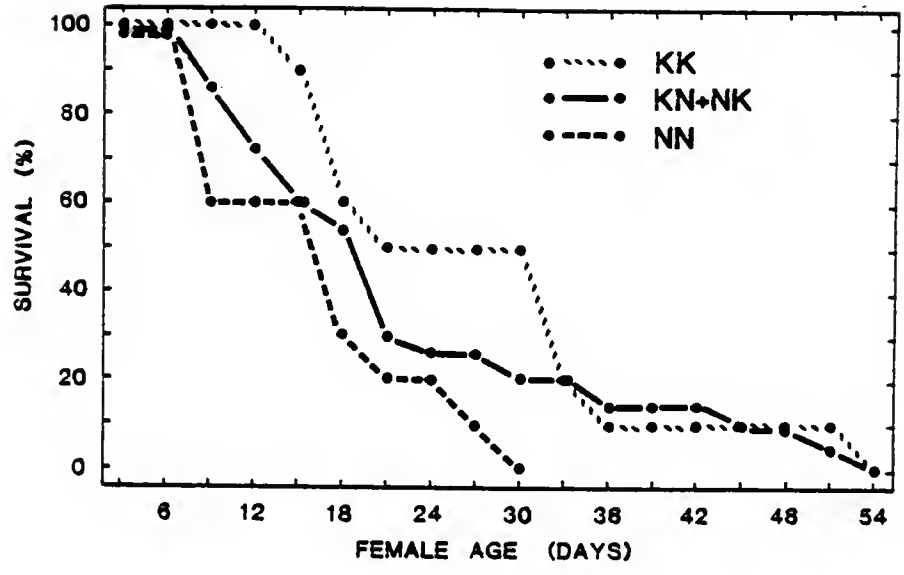

Fig. 3-1. Survival curves (% alive) of Ips calligraphus females in slash pine bolts at 30°C by treatment; KK= 10 females maintained on thick (2.5-3.5) phloem only, KN+NK = 20 females switched between thick and thin (1.0-1.5 mm) phloem at 3-day intervals, and NN = females maintained on thin phloem only.

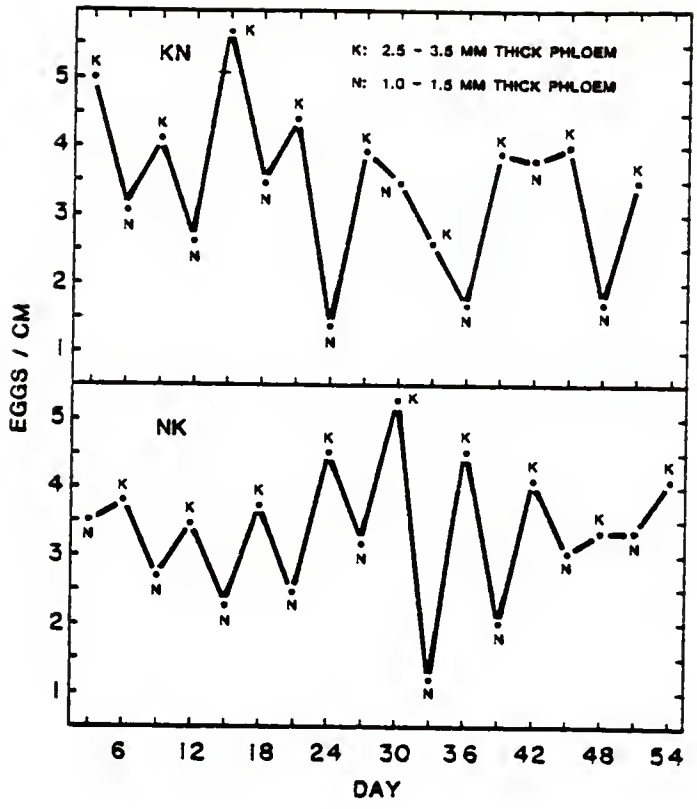

Fig. 3-2. Egg density (eggs/cm of gallery) averaged over 3-day periods throughout the lives of Ips calligraphus females that were switched every 3 days between slash pine bolts having either thick (K; 2.5-3.5 mm) or thin (N, 1.0-1.5 mm) phloem at 30°C. N = 10 females/treatment initially; see Table 3-2 for "N" values pertaining to the number of females alive on a given day.

Table 3-1. Longevity, total gallery length (TGL), gallery construction rate (GCR), fecundity, oviposition rate (OR), and egg density of *Ips calligraphus* females maintained in slash pine bolts at 30°C by treatment.

Parameter	Treatment[1] KK $\bar{X} \pm$ SD (Range)	KN+NK $\bar{X} \pm$ SD (Range)	NN $\bar{X} \pm$ SD (Range)
Longevity (days)	29.1±12.3a[2] (14 - 54)	23.0±14.0ab (9 - 54)	17.5±7.9b (9 - 30)
TGL (cm)	75.8±20.4a (44 - 113)	73.8±33.6a (32 - 149)	55.8±25.0a (24 - 101)
GCR (mm/day)	27.9±6.1b (21 - 40)	34.6±6.2a (24 - 44)	32.4±4.9ab (24 - 41)
Fecundity (eggs)	326±104a (156 - 464)	263±120a (80 - 572)	160±70b (58 - 280)
OR (eggs/day)	11.8±2.8a (9 - 17)	12.4±2.7a (8 - 17)	9.3±1.6b (6 - 11)
ED (eggs/cm)	4.3±0.8a (3.5 - 5.9)	3.6±0.5b (2.5 - 4.8)	2.9±0.3c (2.2 - 3.2)

[1]KK=10 females maintained on thick (2.5-3.5 mm) phloem only; KN+NK=20 females switched between thick and thin (1.0-1.5 mm) phloem at 3-day intervals; and NN=10 females maintained on thin phloem only.

[2]Means followed by the same letter (within rows) are not significantly different at the $P<0.05$ level ($P<0.01$ for ED) (Duncan's multiple-range test).

Table 3-2. Percent of Ips calligraphus females that were alive at the end of each 3-day oviposition period when maintained in slash pine bolts at 30°C by treatment.

Time Periods (Days)	Percent Alive by Treatment[1]			
	KK (N=10)	KN (N=10)	NK (N=10)	NN (N=10)
1-3	100	100	100	100
4-6	100	100	100	100
7-9	100	100	100	100
10-12	100	100	70	60
13-15	100	70	70	60
16-18	90	60	60	60
19-21	60	60	50	30
22-24	50	30	30	20
25-27	50	20	30	20
28-30	50	20	30	10
31-33	50	20	20	0
34-36	20	20	20	0
37-39	10	10	20	0
40-42	10	10	20	0
43-45	10	10	20	0
46-48	10	10	10	0
49-51	10	10	10	0
52-54	10	0	10	0
55-57	0	0	0	0

[1]KK=females maintained on thick (2.5-3.5 mm) phloem only; KN=females switched between thick and thin (1.0-1.5 mm) phloem at 3-day intervals beginning on thick phloem; NK= females switched between thick and thin phloem at 3-day intervals beginning on thin phloem; and NN=females maintained on thin phloem only.

Table 3-3. Linear equations, levels of significance (P), and coefficients of determination (r^2) for regression analyses of Ips calligraphus female survival (lx; percent alive at beginning of day x), gallery construction rate (GCR; mm/day), oviposition rate (OR; eggs/day), and egg density (ED; eggs/cm) with female age (D; days) at 30°C by treatment and overall.

Treatment*	N**	Equation	P<	r^2
Survival				
KK	18	lx = 116 - 2.27 D	0.01	0.91
KN+NK	35	lx = 101 - 2.07 D	0.01	0.86
NN	10	lx = 118 - 3.76 D	0.01	0.93
Overall	63	lx = 103 - 2.12 D	0.01	0.83
Gallery Construction Rate				
KK	98	GCR = 42.03 - 0.87 D	0.01	0.65
KN+NK	151	GCR = 42.24 - 0.61 D	0.01	0.41
NN	62	GCR = 42.26 - 0.93 D	0.01	0.42
Overall	311	GCR = 41.72 - 0.72 D	0.01	0.47
Oviposition Rate				
KK	98	OR = 20.00 - 0.48 D	0.01	0.64
KN+NK	151	OR = 15.29 - 0.24 D	0.01	0.28
NN	62	OR = 15.38 - 0.55 D	0.01	0.49
Overall	311	OR = 15.96 - 0.32 D	0.01	0.35
Egg Density				
KK	98	ED = 5.55 - 0.10 D	0.01	0.32
KN+NK	151	ED = 3.72 - 0.02 D	0.11	0.02
NN	62	ED = 3.80 - 0.10 D	0.01	0.29
Overall	311	ED = 4.05 - 0.04 D	0.01	0.08

*KK=10 females maintained on thick (2.5-3.5 mm) phloem only; KN+NK=20 females switched between thick and thin (1.0-1.5 mm) phloem at 3-day intervals beginning on either thick or thin phloem, respectively; and NN=10 females maintained on thin phloem only.

**N for "Survival" = number of 3-day intervals during which females were alive by treatment, and N for "GCR," "OR," and "ED" = number of egg galleries on which observations were made by treatment.

Table 3-4. Gallery construction rate (mm/day; mean ± SD) over 3-day periods throughout the lives of Ips calligraphus females in slash pine bolts at 30°C by treatment.

Time Periods (Days)	Gallery Construction Rate by Treatment[1]			
	KK	KN	NK	NN
1-3	35 ± 5ab2[2]	30 ± 6abcd3	42 ± 6a1	40 ± 4ab12
4-6	40 ± 4ab1	42 ± 7a1	38 ±10a1	41 ± 6a1
7-9	42 ± 5a1	40 ± 7ab1	42 ± 9a1	33 ± 8abc2
10-12	30 ± 8abc2	35 ± 8abcd12	40 ± 6a1	28 ±11bcd2
13-15	28 ±10bc1	29 ± 9abcd1	34 ±11ab1	26 ± 9cd1
16-18	27 ±10bcd1	27 ±14abcd1	29 ±11abc1	27 ± 9cd1
19-21	26 ± 9bcd2	31 ± 8abcd12	36 ± 7ab1	16 ± 5d3
22-24	17 ± 7cde1	24 ±16abcde1	25 ±10abcd1	25 ±12cd1
25-27	11 ± 3e2	19 ±10cde12	28 ± 6abcd1	26 ± 8cd1
28-30	12 ± 5e2	38 ±12abc1	18 ± 5bcd2	20 ±12d2
31-33	9 ± 3e	20 ±11bcde	16 ±16cd	-
34-36	11 ± 3e	15 ± 9de	17 ± 9bcd	-
37-39	8 e	28 abcd	18 ± 4bcd	-
40-42	13 e	18 cde	16 ± 1cd	-
43-45	8 e	15 de	18 ± 1bcd	-
46-48	5 e	6 e	17 bcd	-
49-51	6 e	20 cde	13 cd	-
52-54	7 e	-	10 d	-

[1]KK=10 females maintained on thick (2.5-3.5 mm) phloem only; KN=10 females switched between thick and thin (1.0-1.5 mm) phloem at 3-day intervals beginning on thick phloem; NK= 10 females switched between thick and thin phloem at 3-day intervals beginning on thin phloem; and NN=10 females maintained on thin phloem only.

[2]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

Table 3-5. Oviposition rate (eggs/day; mean ± SD) over 3-day periods throughout the lives of Ips calligraphus females in slash pine bolts at 30°C by treatment.

Time Periods (days)	Oviposition Rate by Treatment[1]			
	KK	KN	NK	NN
1-3	17 ± 3a1[2]	15 ± 5ab1	15 ± 2ab1	16 ± 2bcd1
4-6	19 ± 2a1	13 ± 3abc2	15 ± 5a2	11 ± 4ab2
7-9	18 ± 3a1	16 ± 3a1	12 ± 5abc2	9 ± 5b2
10-12	14 ± 5ab12	9 ± 5abcd23	15 ± 3a1	7 ± 5bc3
13-15	13 ± 6abc12	16 ± 3a1	8 ± 5abc23	7 ± 4bcd3
16-18	11 ± 5abc1	10 ± 5abcd1	10 ± 6abc1	8 ± 5bc1
19-21	10 ± 7abcd1	14 ± 5abc1	9 ± 3abc1	2 ± 1cd2
22-24	7 ± 5bcde1	9 ± 7bcd1	11 ± 5abc1	5 ± 6bcd1
25-27	6 ± 4bcde1	8 ± 5abcd1	9 ± 4abc1	2 ± 3cd1
28-30	4 ± 3cde2	13 ± 2abc1	9 ± 2abc1	1 ± 1d2
31-33	2 ± 2de	7 ± 10abcd	3 ± 5c	-
34-36	1 ± 2de	4 ± 5cd	8 ± 1abc	-
37-39	2 e	11 abcd	3 ± 4c	-
40-42	0 e	7 abcd	7 ± 1abc	-
43-45	1 e	6 abcd	5 ± 3c	-
46-48	0 e	1 d	6 bc	-
49-51	0 e	7 abcd	4 c	-
52-54	0 e	-	4 c	-

[1]KK=10 females maintained on thick (2.5-3.5 mm) phloem only; KN=10 females switched between thick and thin (1.0-1.5 mm) phloem at 3-day intervals beginning on thick phloem; NK=10 females switched between thick and thin phloem at 3-day intervals beginning on thin phloem; and NN=10 females maintained on thin phloem only.

[2]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

Table 3-6. Egg density (eggs/cm of gallery beginning at the first egg; mean ± SD) over 3-day periods throughout the lives of *Ips calligraphus* females in slash pine bolts at 30°C by treatment.

Time Periods (Days)	Egg Density by Treatment[1]			
	KK	KN	NK	NN
1-3	4.9±1.3a1[2]	5.0±1.8ab1	3.5±0.6abcd2	4.1±0.6a12
4-6	4.8±0.5a1	3.1±0.6abcd3	3.8±0.7abcd2	2.7±0.8abc3
7-9	4.2±0.6abc1	4.1±0.9abcd1	2.7±0.8bcde2	2.6±1.1abc2
10-12	4.6±1.6ab1	2.6±1.0bcd2	3.8±0.4abcd1	2.1±1.4bc2
13-15	4.1±1.6abc1	5.7±1.0a1	2.3±1.1cde2	2.4±1.2abc2
16-18	4.3±1.5abc1	3.5±0.7abcd12	3.7±2.0abcd12	2.6±1.3abc2
19-21	3.7±2.2abc12	4.4±1.1abc1	2.4±0.7cde23	1.0±0.9cd3
22-24	3.5±1.9abc1	1.4±1.6d1	4.5±0.5ab1	3.0±3.7ab1
25-27	5.0±3.1a1	3.9±0.3abcd1	3.2±0.9bcd1	1.0±1.4cd1
28-30	3.6±2.2abc12	3.5±0.6abcd12	5.3±0.8a1	0.3±0.03d2
31-33	1.4±1.8abcd	2.5±3.6bcd	1.2±1.7e	-
34-36	1.1±1.3bcd	1.8±2.5cd	4.5±0.2ab	-
37-39	2.0 abcd	3.9 abcd	2.0±2.8de	-
40-42	0.0 d	3.8 abcd	4.1±1.1abc	-
43-45	0.8 cd	4.0 abcd	3.0±1.9bcde	-
46-48	0.0 d	1.7 cd	3.3 abcd	-
49-51	0.0 d	3.5 abcd	3.3 abcd	-
51-54	0.0 d	-	4.1 abc	-

[1]KK=10 females maintained on thick (2.5-3.5 mm) phloem only; KN=10 females switched between thick and thin (1.0-1.5 mm) phloem at 3-day intervals beginning on thick phloem; NK=10 females switched between thick and thin phloem at 3-day intervals beginning on thin phloem; and NN=10 females maintained on thin phloem only.

[2]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

Discussion

The observed variations in I. calligraphus longevity and fecundity are probably related to (1) differences in the physical and nutritional nature of xylem, phloem, and outer bark and, (2) differences in the relative proportions of these tissues that are encountered when females tunnel in thin versus thick phloem. As was discussed in chapter II, xylem in pines consists mostly of thick-walled, heavily lignified, nutrient-poor cells; outer bark consists mostly of heavily suberized, slightly lignified, nutrient-poor cells; and phloem consists mostly of thin-walled, unlignified, unsuberized, nutrient-rich cells (Howard 1971; Kramer and Kozlowski 1979). In slash pine, average water content is 69% in phloem (Martin 1969), 47% in xylem (Miller 1959), and 20% in outer bark (Martin 1969). Similar values were reported by Wagner et al. (1979) for uninfested loblolly pine, Pinus taeda L.; being ca. 69% in phloem, 44% in xylem, and 23% in outer bark.

Considering the above tissue characteristics and that I. calligraphus is a liquid-feeder (Gouger et al. 1975), it appears likely that females would expend more energy and obtain fewer nutrients per cm of gallery when tunneling in thin phloem because they would be forced to mine more xylem and outer bark. Females in thick phloem, however, would probably acquire nutrients with relative ease, expend less energy in egg production, and thus could allocate more total

resources to egg production. Indeed, Reid (1962) reported that D. ponderosae oviposition rate dropped with declining phloem water content (PWC), and that oviposition ceased when PWC fell below ca. 51%. The above scenarios may partially explain why I. calligraphus longevity, fecundity, OR, and ED are lower for females in thin phloem.

The fact that females lay more eggs per cm of gallery when switched from thin to thick phloem and then lay fewer when moved back again (Fig. 3-2) indicates (1) that reproduction is strongly influenced by host characteristics, and (2) that changes in reproduction occur rapidly when a different host environment is encountered. Also, the decline in egg density along the length of the gallery when females were switched from thick to thin phloem suggests that nutrients are accumulated when in thick phloem and subsequently used during initial oviposition when in thin phloem. As a result, egg density decreases over time after transfer to thin phloem. Similarly, initial reproduction in thick phloem appears to be affected by the presumed physical and nutritional constraints that are encountered in thin phloem; that is, egg density increases over time after females are transfered from thin to thick phloem.

Another point to consider is that very few galleries contained any appreciable length of terminal egg-free gallery; when it did occur the phloem thickness class in which the gallery had been constructed was almost invariably

"thin." Thus, the OR and ED values presented in this chapter probably approach the upper limits attainable by this bark beetle species; that is, because females were widely spaced and removed before reaching the bolt ends, they did not encounter any apparent intraspecific competition, associated microorganisms from other galleries, or discolored phloem, all of which are known to lower oviposition in bark beetles (McMullen and Atkins 1961; Franklin 1970; Amman 1972; Yearian et al. 1972; Thomson and Sahota 1981; Wagner et al. 1982). Because the above factors were minimized by the experimental design of this study, it seems logical that the differences in reproductive performance observed in this study are best explained in terms of the aforementioned nutritional and physical constraints to boring in thin versus thick phloem.

Summary

In summary, the following points can be made with respect to I. calligraphus longevity and fecundity in relation to slash pine phloem thickness.

1. Females live longer when constructing egg gallery in thicker phloem.
2. Total length of gallery constructed per female lifetime is apparently little affected by phloem thickness.
3. Realized fecundity is greater in thicker phloem.

4. The number of eggs laid per unit time as well as the number laid per unit length of gallery is greater for females in thicker phloem.
5. Female reproduction can apparently be modified by a new host environment within a single day.
6. Such results demonstrate the potential influence the host tree can have on biological parameters of relatively large phloem-feeding insects such as I. calligraphus. Great care should therefore be exercised when selecting host materials for bark beetles studies, especially if phloem thickness ranges from thinner to thicker than the average width of females used in a study.

CHAPTER IV
IPS CALLIGRAPHUS RE-EMERGENCE, BROOD DEVELOPMENT, BROOD PRODUCTION PER PARENT FEMALE, AND BROOD-ADULT EMERGENCE, PRONOTAL WIDTH, AND SEX RATIO IN RELATION TO TEMPERATURE AND SLASH PINE PHLOEM THICKNESS

Introduction

The studies described in chapters II and III have shown that slash pine phloem thickness has a profound effect on I. calligraphus reproductive performance. The question as to whether or not variation in phloem thickness also affects parent adult re-emergence, brood developmental time, brood production per parent female, and brood adult emergence, pronotal width (a measure of body size), and sex ratio naturally followed.

Relatively little has been published on the re-emergence process in Ips bark beetles (Foltz et al. 1984). This is in sharp contrast to the abundant information on re-emergence by the southern pine beetle, Dendroctonus frontalis (Cooper and Stephen 1978; Wagner et al. 1981a, 1981b; Gagne et al. 1982). Several accounts of I. calligraphus development are found in the literature (Dale 1967; Yearian and Wilkinson 1967; Yearian et al. 1972; Ascencio 1979). Overall, these studies described the effects of temperature, diet and/or symbionts on rate of brood development. Data were presented

by Dale (1967) on brood production per parent female and times to 50% brood emergence for I. calligraphus reared at several temperatures. He also reported average pronotal-width values of 1.6-1.8 mm for brood adults. In several studies a 1:1 sex ratio has been reported for I. calligraphus brood adults (Wray 1951; Dale 1967; Cook et al. 1983).

Several laboratory studies were conducted during 1981 in order to investigate the relationship between slash pine phloem thickness and the above parent adult and brood parameters. The results of these studies will be discussed in this chapter.

Methods and Materials

Bolt and bark slab preparation. Rearing materials were prepared from 20-year-old slash pine trees growing in a plantation with a site index of 58 ft (17.6 m) at 25 years, near Orange Heights, Alachua County, Florida. Sixteen trees were felled between 12 April and 30 September 1981. Phloem thickness along the trunk measured 0.5-1.5 mm on 7 of these trees, and 2.5-3.5 mm on the other 9 trees. These phloem-thickness ranges were considered, respectively, "thin" and "thick" relative to the average pronotal width of I. calligraphus adults; average pronotal width for Florida populations range between 1.7-1.8 mm (see chapter II). After felling, bolts (30-35 cm long) were cut from the lower

trunk of each tree, end-dipped in a benomyl fungicide-water solution (1%), and dried for 3-4 days at 40-42°C and 40-50% RH. Following drying, the loose outer-bark flakes were removed and the bolt ends were pared back until unstained phloem was detected. Those rearing materials that were used as bolts were then end-dipped in melted paraffin. However, in the case of bark slabs, a few of the bolts were subsequently grooved on a table saw, with the bark slabs (30-34 cm long, 10-14 cm wide, 2-4 cm thick) then cut away by splitting with ax and hammer. Each slab was coated with paraffin on all cut surfaces. Bolts and slabs were stored at 20°C until used.

Source of experimental beetles. Parent adults were reared from 15- and 20-year-old slash pine trees having thick phloem; 6 trees were cut in all. These trees were felled throughout the period of study and allowed to undergo natural infestation by I. calligraphus. When most of the developing brood reached the pupal stage, infested sections were taken to the laboratory and stored in outdoor emergence cages. Emerging brood adults were collected several times daily, sexed according to the form of the third elytral tooth (Hopping 1963), put into containers with moist paper towels, and stored at 20°C until used.

In two studies, brood adults reared from thick- and thin-phloem bolts at 30°C (first filial generation = F1), were used as parent adults to produce the subsequent F2

generation. As above, the F1 brood adults were collected and sexed daily, and stored at 20°C until used.

Introduction of beetles into bolts and bark slabs. Only mature, non-injured adults that were collected within 48 h prior to the time of introduction were used as parent adults. Following the methods of Wilkinson (1964), "starter holes" were drilled obliquely through the outer bark and into the underlying phloem. Two starter holes were made on opposing sides of each bolt along the mid-line. A single adult male was placed into the long section of a size 00 gelatin capsule that had been pierced on the end for ventilation and contained a ring of paper for footing. The capsule was secured over the starter hole with a ring of Duxseal(R) sealing compound. Males not actively boring within 1 h after introduction were replaced. Males were allowed about 24 h to construct a nuptial chamber at 30°C. Three females were serially introduced into each nuptial chamber at 30-45 min intervals as described above. The infested bolts and slabs were randomly assigned to 1 of 3 temperature treatments (20°, 25°, 30°C), and stored in ventilated rearing cans (photoperiod 12L:12D; 55-70% RH). These temperatures were selected because in Alachua County, Florida, summer temperatures can average near 30°C, while in spring and fall they average near 20°C (Dohrenwend 1978).

With respect to the F1-F2 study, F1 adults from the 30°C treatment that had been collected within 24 h prior to the

time of introduction were used as parent adults. The F1 adults were introduced into thick-phloem bolts using the procedures and sex ratios described above, and held at 30°C.

Data collection. *Ips calligraphus* egg gallery construction and brood development were monitored by x-raying slabs with a Faxitron(R) X-ray unit and Kodak(R) AA film. Infested slabs were radiographed at regular intervals throughout the period of oviposition and subsequent brood development. Re-emergence of parent adults was tallied daily. The numbers of larvae, pupae, and young brood adults observed on each radiograph were recorded on a per-slab and per parent-female basis. Following the last day of radiography, a portion of the slabs were frozen while the others were left to allow for brood adult emergence. The frozen slabs were later dissected to obtain values of initial oviposition. An acetate tracing was made of each dissected slab to show the nuptial chamber, egg galleries, and egg niches. Brood adult emergence was tallied daily. Developmental time was recorded in days starting from the date of parent female introduction. Production of brood adults was recorded on a per parent-female basis. Bolts and slabs were dissected after brood emergence had ceased in order to record the actual number of egg galleries and egg niches from which the individuals had originated. This was done to avoid counting those parent females that had either re-emerged or died before producing brood. All brood adults

were sexed, and from a sample of these adults, the pronotal width was measured using a microscope with ocular micrometer.

In the F1-F2 study, bolts were debarked when most of the F2 brood reached the adult stage and all individuals were collected. The pronotal width and sex of the F2 brood adults were determined from samples of adults representing each rearing bolt. The F2 sex ratio was expressed on a per-bolt basis.

Analyses. Data were analyzed with the t-test and general linear models procedures of the Statistical Analysis System (SAS), version 1982.3. Preliminary analyses, using the t-test, indicated no significant ($P>0.05$) differences between experiments conducted in bolts and slabs of the same phloem thickness with respect to parent adult re-emergence, brood developmental time, and brood adult emergence time, pronotal width, and sex ratio. These data were thus pooled in subsequent analyses.

Re-emergence of parent adults was compared between sexes, phloem thickness classes, and among temperature treatments, using the t-test and Duncan's multiple-range test. Regression analysis of re-emergence times was performed with temperature for parent males and females separately. Brood development in thick and thin phloem was analyzed within each temperature treatment by comparing the proportions of larvae, pupae, and brood adults found at various times

throughout their development. These data were analyzed after arcsin transformation (Steel and Torrie 1980). Brood production per parent female and times to 50% emergence of the F1 brood adults were compared between phloem thickness classes and among temperatures using the t-test and Duncan's multiple-range test. Regression of average developmental time was performed with temperature for thick and thin phloem separately. Pronotal widths and sex ratios of the F1 and F2 brood adults were compared between sexes, phloem thickness classes, and generations using the t-test. Sex ratios were expressed as a percent and analyzed without transformation by the t-test.

Results

Re-emergence of parent adults. The average number of days to 50% re-emergence of parent males and females did not differ significantly ($P>0.10$) between phloem thickness classes, and thus these data were pooled within each sex. On the average, parent males re-emerged about 1-2 days earlier than parent females (Table 4-1). Overall, 90-100% of the males and 89-100% of the females re-emerged from the bolts and slabs used in the various studies. Average time to 50% re-emergence decreased with increasing temperature (Table 4-1). Regression equations of time to 50% re-emergence (R, days) with temperature (°C) are $R = 54.66 - 1.56°C$ for males ($r^2=0.71$, $Sy.x=0.11$, N=87 males), and R =

55.21 - 1.50°C for females (r^2=0.71, Sy.x=0.07, N=197 females).

Brood development. Brood developed faster in thick phloem than in thin phloem at each of the 3 temperatures tested (Table 4-2). The radiographs made late during development revealed significantly ($P<0.05$) more individuals in the pupal and adult stages in thick versus thin phloem.

Brood development in thick phloem is presented on a per female-parent basis in Figs. 4-1 (20°), 4-2 (25°), and 4-3 (30°C). In this particular study, cumulative oviposition (%) at 20°, 25°, and 30°C was, respectively, 3, 8, and 15% on day 1; 13, 27, and 37% on day 2; 40, 65, and 80% on day 4; and 71, 98, and 100% on day 8. Cumulative oviposition reached 100% by day 16 at 25° and by day 24 at 20°C. Egg hatch occurred after about 6, 3, and 2 days at 20°, 25°, and 30°C, respectively, based on daily dissections of other similarly-prepared bark slabs.

Brood adult production per parent female. More F1 brood adults emerged per parent female from thick phloem than from thin phloem (Table 4-3). Brood production was largest in thick phloem at 30°C, and smallest in thin phloem at 20°C.

Brood adult emergence. Average time to 50% emergence of brood adults was about 3-4 days sooner on thick versus thin phloem (Table 4-4). Brood emergence, expressed as brood adults/parent female/day, is presented in Tables 4-5 (20°),

4-6 (25°), and 4-7 (30°C). Time to 50% adult emergence was inversely correlated with temperature. Regression equations for time to 50% brood emergence (E, days) with temperature (°C) are E = 108.00 - 2.78°C in thick phloem (r^2=0.82, Sy.x=0.02, N=3090 brood adults from 69 brood cohorts), and E = 110.63 - 2.75°C in thin phloem (r^2=0.83, Sy.x=0.04, N=1006 and 42).

Brood adult pronotal width. Pronotal widths of F1 males and females from thick phloem were 8 and 6% larger, respectively, than those for the same sex from thin phloem (Table 4-8). Males were significantly ($P<0.01$) wider (ca. 5%) than females when reared from thick phloem. However, when reared in thin phloem, males and females had similar pronotal widths ($P>0.49$). With respect to the F2 brood adults, who all developed in thick phloem, pronotal width was not influenced by parental phloem thickness (Table 4-8). That is, progeny of the thin-phloem reared F1 adults were as large as progeny of thick-phloem reared F1 adults.

Brood adult sex ratio. The sex ratio was approximately 1:1 (males:females) for F1 brood adults reared from thick phloem. In thin phloem, the sex ratio was skewed in favor of females, being ca. 1:2 (Table 4-9). In the F2 generation, where all development occurred on thick phloem, the sex ratio of progeny from both thick- and thin-phloem reared adults was 1:1.

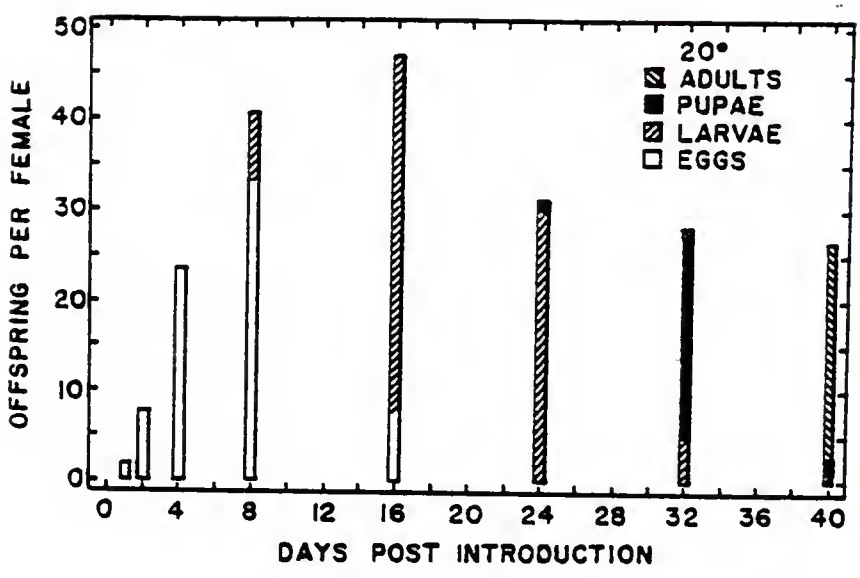

Fig. 4-1. Ips calligraphus brood stages (no. offspring per parent female) through time at 20°C in slash pine bark slabs (N=7) with thick (2.5-3.5 mm) phloem. Life stages were determined from inspection of radiographs taken on various days (after parent-female introduction) throughout the period of brood development.

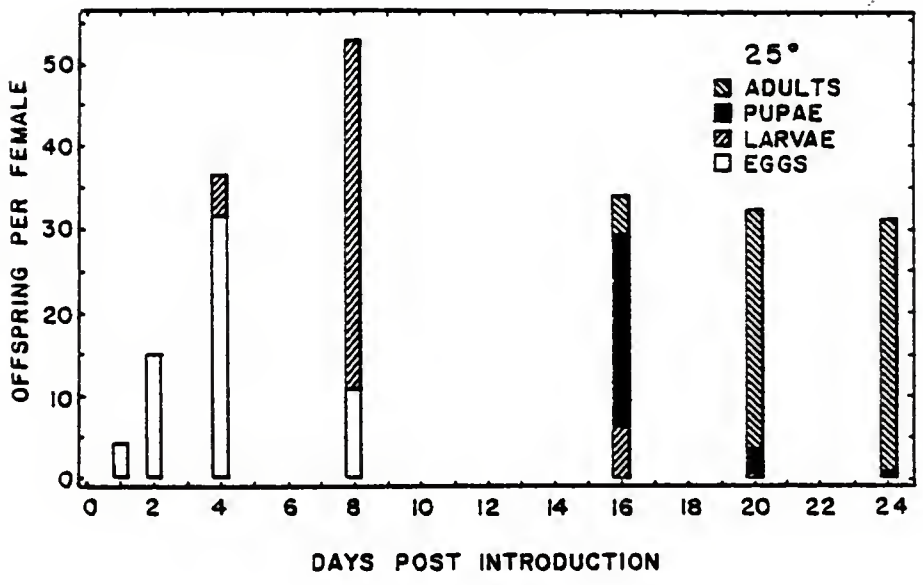

Fig. 4-2. Ips calligraphus brood stages (no. offspring per parent female) through time at 25°C in slash pine bark slabs (N=7) with thick (2.5-3.5 mm) phloem. Life stages were determined from inspection of radiographs taken on various days (after parent-female introduction) throughout the period of brood development.

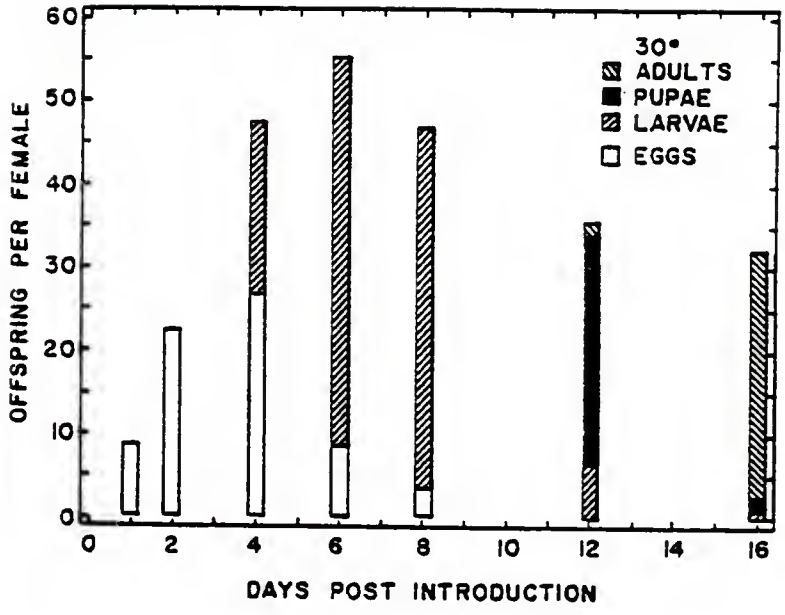

Fig. 4-3. Ips calligraphus brood stages (no. offspring per parent female) through time at 30°C in slash pine bark slabs (N=7) with thick (2.5-3.5 mm) phloem. Life stages were determined from inspection of radiographs taken on various days (after parent-female introduction) throughout the period of brood development.

Table 4-1. Average number of days to 50% re-emergence of Ips calligraphus male and female parent adults, starting from the time of parent female introduction, in slash pine bolts and slabs and maintained at 20°, 25°, or 30°C.

	Re-emergence (Days)			
	Male		Female	
°C	N	$\bar{X} \pm SD$[1] (Range)	N	$\bar{X} \pm SD$ (Range)
20°	28	24.3 ± 5.4a1 (16 - 35)	68	25.9 ± 5.5a1 (18 - 37)
25°	30	14.1 ± 3.6b2 (8 - 20)	57	15.7 ± 3.0b1 (10 - 20)
30°	29	8.6 ± 2.4c2 (6 - 15)	72	10.9 ± 2.4c1 (6 - 15)

[1]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple range test).

Table 4-2. Percent of Ips calligraphus brood individuals (I) found in the larval, pupal, and adult stages in slash pine slabs with thick (TK, 2.5-3.5 mm) or thin (TN, 0.5-1.5 mm) phloem on various days after parent female introduction at 20°, 25°, and 30°C.

°C	Day	Phloem	N[1] I	N[1] S	Larval $\bar{X} \pm$ SD[2]	Pupal $\bar{X} \pm$ SD	Adult $\bar{X} \pm$ SD
20°							
	28	TK	158	3	51 ± 19b	49 ± 19a	0 a
		TN	116	4	95 ± 4a	5 ± 4b	0 a
	32[3]	TK	533	7	18 ± 11	80 ± 11	3 ± 3
	35	TK	163	3	6 ± 4b	32 ± 13a	62 ± 17a
			101	4	52 ± 36a	40 ± 31a	8 ± 9b
	40[3]	TK	507	7	2 ± 2	9 ± 4	89 ± 4
25°							
	16	TK	854	9	31 ± 10b	63 ± 12a	7 ± 6a
		TN	189	5	93 ± 5a	6 ± 4b	1 ± 1b
	20	TK	824	9	4 ± 4b	11 ± 4b	85 ± 6a
		TN	188	5	49 ± 21a	48 ± 20a	3 ± 3b
30°							
	12	TK	1035	10	30 ± 12b	66 ± 10a	4 ± 4a
		TN	194	4	90 ± 16a	10 ± 16b	0 b
	16	TK	981	11	3 ± 2b	5 ± 3b	92 ± 4a
		TN	185	4	63 ± 24a	29 ± 15a	9 ± 14b

[1]I=number of individuals counted; S=number of slabs used.

[2]Means followed by the same letter (within columns, by life stage and day) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

[3]Only slabs with thick phloem were radiographed on days 32 and 40 in the 20°C treatment.

Table 4-3. *Ips calligraphus* brood adults (F1) per parent female from slash pine bolts and slabs with thick (2.5-3.5 mm) or thin (0.5-1.5 mm) phloem and maintained at 20°, 25°, or 30°C.

	Brood Adults / Parent Female					
	Thick Phloem			Thin Phloem		
	N[1]			N		
°C	F1	P	$\bar{X} \pm SD$[2] (Range)	F1	P	$\bar{X} \pm SD$ (Range)
20°	607	18	33.7 ± 10.9b1 (13 - 44)	158	9	17.6 ± 2.9b2 (15 - 21)
25°	556	15	37.1 ± 10.9b1 (22 - 55)	229	9	25.4 ± 5.0a2 (18 - 29)
30°	1927	36	53.5 ± 17.8a1 (22 - 74)	619	25	25.8 ± 5.8a2 (16 - 33)

[1]F1=number of brood adults that emerged; P=number of parent females that constructed egg galleries and oviposited.

[2]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

Table 4-4. Number of days to 50% emergence of Ips calligraphus brood adults (F1) , starting from the time of parent female introduction, in slash pine bolts and slabs with thick (2.5-3.5 mm) or thin (0.5-1.5 mm) phloem and maintained at 20°, 25°, or 30°C.

	Brood Emergence (Days)					
	Thick Phloem			Thin Phloem		
	N[1]			N		
°C	F1	S	$\bar{X} \pm SD$[2] (Range)	F1	S	$\bar{X} \pm SD$ (Range)
20°	607	7	55.0 ± 5.1a2 (47 - 68)	158	3	58.5 ± 4.5a1 (51 - 70)
25°	556	7	33.1 ± 5.6b2 (25 -50)	229	3	37.9 ± 4.8b1 (29 - 50)
30°	1927	11	25.5 ± 3.8c2 (17 - 37)	619	9	28.8 ± 3.8c1 (22 - 38)

[1]F1=number of brood adults that emerged; S=number of bolts and/or slabs used.

[2]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.01$ level (Duncan's multiple-range test).

Table 4-5. Average number of Ips calligraphus brood adults per parent female per day that emerged from slash pine bolts and slabs with thick (2.5-3.5 mm) or thin (0.5-1.5 mm) phloem at 20°C.

	Brood Adults / Parent Female[1] / Day at 20°C					
	Thick Phloem			Thin Phloem		
Day[2]	N[3]	$\bar{X} \pm SD$[4]	Range[5]	N	$\bar{X} \pm SD$	Range
47	18	1.0 ± 1.0	(0.0-2.3)	0		
48	24	1.2 ± 1.2	(0.0-2.7)	0		
49	36	1.8 ± 2.0	(0.0-5.3)	0		
50	47	2.4 ± 2.0	(1.0-6.0)	0		
51	49	2.4 ± 2.0	(0.0-5.7)	6	0.7 ± 0.3	(0.5-1.0)
52	50	2.4 ± 1.4	(0.0-4.0)	8	0.9 ± 0.4	(0.5-1.3)
53	42	2.1 ± 1.0	(0.0-3.0)	9	1.0 ± 0.6	(0.5-1.7)
54	45	2.6 ± 0.4	(2.0-3.0)	10	1.0 ± 1.2	(0.0-2.3)
55	51	2.8 ± 0.6	(2.0-4.0)	15	1.7 ± 0.6	(1.3-2.3)
56	52	2.6 ± 1.5	(1.0-5.3)	16	1.9 ± 0.6	(1.3-2.3)
57	29	1.5 ± 1.1	(0.7-4.0)	8	1.0 ± 0.1	(0.8-1.0)
58	27	1.4 ± 1.3	(0.0-4.0)	8	1.0 ± 0.5	(0.7-1.5)
59	19	1.0 ± 0.8	(0.0-2.3)	11	1.0 ± 0.9	(0.0-1.8)
60	18	1.2 ± 1.0	(0.3-3.0)	11	1.1 ± 0.5	(0.5-1.5)
61	17	1.1 ± 0.6	(0.3-2.0)	14	1.7 ± 0.8	(1.0-2.5)
62	12	0.8 ± 1.1	(0.0-3.0)	14	1.7 ± 0.7	(1.3-2.5)
63	20	1.5 ± 1.4	(0.0-4.0)	8	0.9 ± 0.1	(0.8-1.0)
64	16	0.9 ± 0.9	(0.0-2.0)	6	0.6 ± 0.1	(0.5-0.8)
65	10	0.5 ± 0.5	(0.0-1.0)	4	0.5 ± 0.4	(0.3-1.0)
66	11	0.4 ± 0.6	(0.0-1.5)	3	0.3 ± 0.3	(0.0-0.5)
67	8	0.3 ± 0.6	(0.0-1.5)	2	0.3 ± 0.3	(0.0-0.5)
68	6	0.2 ± 0.4	(0.0-1.0)	1	0.1 ± 0.2	(0.0-0.3)
69	0			2	0.3 ± 0.3	(0.0-0.5)
70	0			2	0.3 ± 0.3	(0.0-0.5)

[1]There were 18 parent females in thick phloem and 9 in thin phloem that constructed egg gallery and oviposited.

[2]Values represent the number of days after parent female introduction.

[3]N=number of brood adults that emerged on the day indicated.

[4]Means were based on the combined data from 7 bolts and/or slabs with thick phloem and 3 with thin phloem.

[5]Values represent the range of values for individual bolts and/or slabs.

Table 4-6. Average number of Ips calligraphus brood adults per parent female per day that emerged from slash pine bolts and slabs with thick (2.5-3.5 mm) or thin (0.5-1.5 mm) phloem at 25°C.

	Brood Adults / Parent Female[1] / Day at 25°C					
	Thick Phloem			Thin Phloem		
Day[2]	N[3]	$\bar{x}$ ± SD[4]	Range[5]	N	$\bar{X}$ ± SD	Range
25	9	0.4 ± 0.6	(0.0-1.5)	0		
26	15	0.8 ± 0.7	(0.0-1.8)	0		
27	42	2.5 ± 2.1	(0.0-5.0)	0		
28	62	3.9 ± 2.4	(0.0-7.0)	0		
29	54	3.4 ± 1.3	(1.0-5.5)	4	0.4 ± 0.8	(0.0-1.3)
30	54	3.4 ± 1.5	(1.0-6.0)	9	0.9 ± 1.2	(0.0-2.3)
31	45	2.9 ± 1.0	(1.0-4.0)	7	0.7 ± 0.9	(0.0-1.7)
32	29	2.0 ± 1.3	(0.5-4.0)	9	0.9 ± 1.0	(0.0-2.0)
33	30	2.1 ± 1.2	(0.5-4.0)	10	1.1 ± 0.6	(0.5-1.7)
34	27	1.9 ± 1.6	(0.0-4.0)	18	1.8 ± 0.8	(1.0-2.5)
35	23	1.6 ± 1.6	(0.0-4.5)	22	2.1 ± 1.5	(0.5-3.5)
36	18	1.3 ± 1.5	(0.0-3.5)	20	1.9 ± 1.7	(0.5-3.8)
37	18	1.4 ± 1.6	(0.0-4.0)	13	1.3 ± 0.8	(0.7-2.3)
38	27	2.1 ± 2.6	(0.0-7.0)	17	1.8 ± 0.6	(1.3-2.5)
39	21	1.6 ± 1.8	(0.0-5.0)	20	2.2 ± 0.8	(1.3-2.8)
40	18	1.3 ± 1.5	(0.0-4.0)	16	1.7 ± 0.8	(1.0-2.5)
41	14	1.0 ± 1.4	(0.0-3.5)	13	1.4 ± 0.3	(1.0-1.7)
42	9	0.5 ± 1.1	(0.0-3.0)	9	0.9 ± 0.7	(0.0-1.3)
43	10	0.7 ± 1.1	(0.0-3.0)	11	1.1 ± 0.6	(0.5-1.7)
44	8	0.7 ± 1.1	(0.0-3.0)	8	1.0 ± 0.5	(0.7-1.5)
45	3	0.1 ± 0.2	(0.0-0.5)	5	0.6 ± 0.3	(0.3-1.0)
46	5	0.5 ± 1.1	(0.0-3.0)	6	0.8 ± 0.6	(0.3-1.5)
47	4	0.5 ± 1.1	(0.0-3.0)	5	0.6 ± 0.3	(0.3-1.0)
48	5	0.4 ± 0.5	(0.0-1.0)	3	0.4 ± 0.5	(0.0-1.0)
49	3	0.1 ± 0.2	(0.0-0.5)	2	0.3 ± 0.3	(0.0-0.5)
50	3	0.2 ± 0.3	(0.0-1.0)	2	0.3 ± 0.6	(0.0-1.0)

[1]There were 15 parent females in thick phloem and 9 in thin phloem that constructed egg gallery and oviposited.

[2]Values represent the number of days after parent female introduction.

[3]N=number of brood adults that emerged on the day indicated.

[4]Means were based on the combined data from 7 bolts and/or slabs with thick phloem and 3 with thin phloem.

[5]Values represent the range of values for individual bolts and/or slabs.

Table 4-7. Average number of Ips calligraphus brood adults per parent female per day that emerged from slash pine bolts and slabs having either thick (2.5-3.5 mm) or thin (0.5-1.5 mm) phloem at 30°C.

	Brood Adults / Parent Female[1] / Day at 30°C					
	Thick Phloem			Thin Phloem		
Day[2]	N[3]	$\bar{x} \pm$ SD[4]	Range[5]	N	$\bar{X} \pm$ SD	Range
17	5	0.2 ± 0.5	(0.0-1.7)	0		
18	19	1.0 ± 1.9	(0.0-6.0)	0		
19	52	1.8 ± 2.2	(0.0-6.0)	0		
20	85	2.8 ± 2.7	(0.0-7.0)	0		
21	131	4.0 ± 2.6	(0.0-7.5)	0		
22	172	4.3 ± 2.7	(2.0-8.8)	4	0.1 ± 0.2	(0.0-0.5)
23	187	5.1 ± 3.9	(0.7-13.0)	17	0.7 ± 1.0	(0.0-2.7)
24	203	5.5 ± 4.6	(0.7-14.0)	59	2.0 ± 1.6	(0.0-4.8)
25	134	3.0 ± 2.9	(0.0-7.0)	63	2.2 ± 1.8	(0.0-5.5)
26	152	3.0 ± 3.0	(0.0-7.0)	53	2.1 ± 1.2	(0.3-4.0)
27	211	4.2 ± 4.8	(0.0-14.3)	72	3.0 ± 1.8	(0.8-6.5)
28	146	2.8 ± 3.8	(0.0-10.3)	40	1.4 ± 0.8	(0.0-2.8)
29	135	2.6 ± 3.4	(0.0-10.0)	47	1.9 ± 0.6	(1.0-3.0)
30	98	1.9 ± 2.4	(0.0-6.3)	73	2.7 ± 1.1	(1.0-4.3)
31	64	1.3 ± 1.8	(0.0-6.0)	42	1.6 ± 1.3	(0.0-4.0)
32	57	1.1 ± 1.9	(0.0-6.0)	42	1.7 ± 1.5	(0.0-4.0)
33	24	0.5 ± 0.7	(0.0-2.0)	31	1.1 ± 0.7	(0.0-2.5)
34	23	0.4 ± 0.7	(0.0-2.0)	26	1.1 ± 0.4	(0.5-2.0)
35	10	0.2 ± 0.3	(0.0-1.0)	10	0.5 ± 0.6	(0.0-1.5)
36	10	0.2 ± 0.4	(0.0-1.0)	11	0.6 ± 0.4	(0.0-1.0)
37	9	0.2 ± 0.2	(0.0-0.5)	21	0.8 ± 0.5	(0.0-1.5)
38	0			8	0.2 ± 0.3	(0.0-0.8)

[1]There were 36 parent females in thick phloem and 24 in thin phloem that constructed egg gallery and oviposited.

[2]Values represent the number of days after parent female introduction.

[3]N=number of brood adults that emerged on the day indicated.

[4]Means were based on the combined data from 11 bolts and/or slabs with thick phloem and 9 with thin phloem.

[5]Values represent the range of values for individual bolts and/or slabs.

Table 4-8. Pronotal width of Ips calligraphus male and female brood adults reared in slash pine bolts having either thick (TK, 2.5-3.5 mm) or thin (TN, 0.5-1.5 mm) phloem (F1 generation), and similarly, by using F1 adults reared at 30°C from both thick and thin phloem as parents, the pronotal width of the F2 brood adults that were reared in thick-phloem bolts at 30°C.

	Pronotal Width (mm)				
	F1 Brood Adults		F1 to F2 Change in Phloem	F2 Brood Adults	
Phloem	N[1]	$\bar{X} \pm SD$[2] (Range)		N	$\bar{X} \pm SD$ (Range)
Males					
TK	50	1.84 ± 0.09a2 (1.7 - 2.1)	TK to TK	50	1.90 ± 0.09a1 (1.7 - 2.1)
TN	50	1.70 ± 0.14b2 (1.4 - 2.0)	TN to TK	50	1.89 ± 0.09a1 (1.7 - 2.1)
Females					
TK	50	1.77 ± 0.08a2 (1.6 - 1.9)	TK to TK	50	1.81 ± 0.08a1 (1.7 - 2.0)
TN	50	1.69 ± 0.08b2 (1.5 - 1.8)	TN to TK	50	1.78 ± 0.08a1 (1.5 - 1.9)

[1]Each sample consisted of 50 randomly-selected adults .

[2]Means followed by the same letter (within columns by sex) or number (within rows) are not significantly dfferent at the $P<0.05$ level (t-test).

Table 4-9. Male proportion of Ips calligraphus brood adults reared from bolts having either thick (TK, 2.5-3.5 mm) or thin (TN, 0.5-1.5) phloem (F1 generation), and similarly, using F1 adults reared at 30°C from both thick and thin phloem as parents, the male proportion of the F2 generation when reared in bolts having thick phloem at 30°C.

	Percent Males						
	F1 Brood Adults			F1 to F2 Change in Phloem	F2 Brood Adults		
Phloem	N[1] I	N[1] B	$\bar{X} \pm SD$[2] (Range)[3]		N I	N B	$\bar{X} \pm SD$ (Range)
TK	1223	12	49.9 ± 4.2a1 (42 - 59)	TK to TK	1005	9	49.2 ± 3.1a1 (45 - 54)
TN	280	5	33.7 ± 5.5b2 (29 - 41)	TN to TK	764	9	50.3 ± 3.4b1 (46 - 56)

[1]I=number of brood adults collected; B=number of bolts used.

[2]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P<0.05$ level (t-test). Means were calculated on a per-bolt basis.

[3]Values represent the range of percents from individual bolts.

Discussion

Re-emergence of Parent Adults

The similarity in time to 50% re-emergence between the 2 phloem thickness classes at a given temperature is related to the rate of gallery construction (GCR) by parent females. Lines of evidence are (1) *I. calligraphus* constructs egg galleries that follow the wood grain (Wilkinson *et al.* 1967), (2) GCR does not vary significantly with changes in phloem thickness (see chapters II and III), and (3) females in both thick and thin phloem reached the bolt and slab extremes (which were similar in length between phloem thickness classes) in about equal times. The radiographs indicated that upon reaching the top or bottom of a slab, females generally stopped ovipositing but continued to construct gallery (terminal egg-free gallery). It was at this time that the females probably changed from a reproductive to a flying condition, and eventually re-emerged. Such changes have been documented in the mountain pine beetle, *Dendroctonus ponderosae* (Reid 1962). These results indicate that re-emergence of *I. calligraphus* parent-adults is strongly influenced by the contiguous length of pine material available and suitable for oviposition.

The close agreement between average times of male re-emergence (Table 4-1) with cumulative 100% oviposition (see "Brood development" section of this chapter) and earlier re-

emergence in males compared to females suggest that males may utilize cessation of oviposition as a signal for re-emergence. Such behavior would maximize a male's reproductive success assuming that he would be (1) guarding and assisting those females with which he had mated during their period of active oviposition, and (2) allowing himself sufficient time to re-emerge, locate other host material, and construct a new nuptial chamber prior to peak female re-emergence.

Development and Brood Adult Characteristics

The observed variations in I. calligraphus developmental time, brood production, and brood adult emergence, pronotal width, and sex ratio are probably related to (1) differences in the physical and nutritional nature of xylem, phloem, and outer bark and (2) differences in the relative proportions of these tissues that are encountered by larvae when tunneling in thin versus thick phloem. As was discussed in chapter II, mostly thick-walled, nutrient-poor cells constitute xylem and outer bark of pines, whereas mostly thin-walled, nutrient-rich cells constitute phloem (Howard 1971; Kramer and Kozlowski 1979). In slash pine, water content averages ca. 69% in phloem (Martin 1969), 44% in xylem (Miller 1959), and 23% in outer bark (Martin 1969).

Thus, the larval environments afforded by host trees with either thick or thin phloem are quite distinct. Larvae in

thin phloem (0.5-1.5 mm), especially last (3rd) instars whose head capsules alone measure ca. 1 mm in width (Wilkinson 1963), must excavate more of the adjacent xylem and/or outer bark than their counterparts in thick phloem. Larvae developing in thin phloem are thus presented with an environment that offers fewer nutrients and water per unit length of gallery constructed, and one that probably also requires more energy to tunnel through. The foregoing scenario explains the protracted development observed in thin phloem, as well as delayed brood emergence. In other studies, developmental time of Tribolium confusum Jacquelin duVal (Coleoptera: Tenebrionidae) was lengthened when larvae were reared on a low- compared to a high-lysine diet (Lamb and Loschiavo 1981). Similarly, developmental time of other Coleoptera is inversely correlated with nitrogen content (Bletchly and Farmer 1959) and moisture content (Cannon and Robinson 1981) of wood.

In thin phloem, I. calligraphus larvae constructed visually longer mines prior to pupation than did larvae in thick phloem. Similar behavior was observed by R. C. Wilkinson[1] (personal communication) in I. calligraphus larvae reared on slash pine foliage-based diets. In diet containing current year's foliage (believed to be of relatively low nutritional quality), larval mines were longer and developmental time was protracted compared to

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[1] Department of Entomology & Nematology, University of Florida, Gainesville, Florida 32611.

larvae on diet containing previous year's foliage. Other results from that study are reported in Richeson *et al.* (1970). *Dendroctonus ponderosae* larvae in thin phloem mined faster than those in thick phloem during the first 2 weeks of larval life (Amman and Cole 1983).

Webb and Franklin (1978) reported that *D. frontalis* produced long larval mines when phloem water content (PWC) was relatively high. In my study, although PWC was not measured in all rearing materials, PWC did not vary significantly ($P>0.10$) between phloem thickness classes (ca. 70% in each). Similar results were reported in chapters II and III. Webb and Franklin (1978) suggested that high PWC was detrimental to the symbiotic bluestain fungus, *Ceratocystis minor* (Hedgc), associated with *D. frontalis*, and thereby indirectly influencing brood survivorship as was shown to occur by Barras (1973). However, in the case of *I. calligraphus*, Yearian *et al.* (1972) successfully reared this species through 4 successive generations in fungus-free slash pine logs. In my study, growth of *Ceratocystis ips* (Rumbold) C. Moreau, the symbiotic bluestain fungus associated with *I. calligraphus*, was apparently similar in thick and thin phloem; *C. ips* perithecia were first observed on the walls of the nuptial chamber on day 6, and along the egg-gallery walls on day 8 following parent-female introduction at 30°C in both thick and thin phloem. Therefore, the observed variations in brood development

recorded in the present study probably cannot be explained in terms of either PWC or C. ips.

Greater brood production/female in thick phloem is probably best explained in terms of greater original egg density (eggs/cm of gallery), than in terms of greater brood survival in thick versus thin phloem. In this study, brood mortality was similar between phloem thickness classes, being ca. 35-50%. As discussed in chapter II, egg density increased with both increasing phloem thickness and temperature. Therefore, assuming equal survival of larvae in thick and thin phloem, the above differences in final brood production are a reflection of greater initial oviposition in thicker phloem.

Dale (1967) reported I. calligraphus brood production values of 15-18 brood adults/female when reared at temperatures between 20°-30°C. He used 30-cm-long bolts from various pine species and infested these at the rate of 2 males and 4 females per bolt. These relatively low brood-production values suggest that thin-phloem rearing materials were used in his study. This very likely would have been the case, because in general the southern pines have relatively thin phloem, averaging about 1.5 mm (Howard 1971).

Larvae in thin phloem had longer developmental times than those reared in thick phloem, and the resulting thin-phloem reared adults were smaller than those reared in thick

phloem. This probably occurred because in thin phloem, more of the ingested food would have been used as an energy source for tunneling and/or body maintenance, instead of being utilized for growth. In the study by Dale (1967), average time to 50% emergence and pronotal width of the brood adults were ca. 45 days and 1.7 mm at 25°, and 29 days and 1.6 mm at 30°C, respectively. Such results, in comparison to the ones presented here, further indicate that the host materials used in Dale's study had relatively thin phloem. Similar results have been reported for D. ponderosae when reared in thin phloem (Amman and Pace 1976; Amman and Cole 1983).

Great variation in adult size has been reported for several wood-inhabiting Coleoptera. Andersen and Nilssen (1983) suggest that such variation in adult size reflects the inability of the wood-feeding larvae to choose and determine their own nutritional situation. That is, adult females may not be able to evaluate and choose the best larval food, and thus by ovipositing on a given host they may force their relatively immobile larvae to develop on materials of low nutritional quality.

Although pronotal width of thick-phloem reared males and females was only slightly larger than that of thin-phloem reared males and females, such differences become magnified when body volume is considered. This occurs because in a cylinder, volume is related to the square of the diameter

(i.e., pronotal width). In another study (F. Slansky Jr.[2] and R. A. Haack, unpublished data), dry weights of brood adults from thick and thin phloem were, respectively, 3.2 mg (±0.4 SD, n=30) and 2.1 (±0.5, n=34) for males, and 2.7 (±0.4, n=35) and 1.9 (±0.3, n=40) for females.

The relatively large size of males compared to females, when reared in thick phloem, is probably associated with differential development times for each sex. Male larvae seem to develop over a longer period of time as indicated by the longer time to 50% emergence of brood males compared to females for the same cohort, and thus they attain a larger final size than do females. This finding was reported by Dale (1967) and was also noted in my study of I. calligraphus voltinism as detailed in chapter V. When development occurs in thin phloem, males seem to be more sensitive than females to the adverse conditions therein. Male size is reduced to a greater extent than is female size, so much that there is no significant difference in final adult body size between the sexes. The importance of phloem thickness is further indicated by the fact that the small size of the thin-phloem reared F1 adults did not affect the final size of their progeny when reared on thick-phloem.

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[2] Department of Entomology & Nematology, University of Florida, Gainesville, Florida 32611.

When considering the biology of I. calligraphus, at least 2 advantages in having males larger than females can be postulated. A larger entry tunnel might enable females to enter the male-constructed nuptial chamber more quickly and thus avoid predators. Also, in those cases where a male has constructed "starter tunnels" away from the nuptial chamber, a female could probably begin oviposition sooner because she would not need to re-bore that length of gallery.

The apparently longer developmental time of males may contribute to the female-biased sex ratio observed in thin phloem. Assuming that the initial sex ratio was 1:1, longer male developmental time may have allowed for greater mortality from cannibalism (by larvae and teneral adults) and/or lower male survival under the adverse conditions of thin phloem. Larvae may be relatively "crowded," in a physical sense, when developing in thin phloem. The effects of larval crowding in various insects include smaller adult size, protracted development, lower survival, and changes from the normal sex ratio (Klomp 1964; Peters and Barbosa 1977). Crowded conditions may also lead to a higher incidence of infection by the bacterium, Serratia marcescens Bizio, in I. calligraphus teneral adults (Jouvenaz and Wilkinson 1970). Amman and Cole (1983) reported lower male survival when D. ponderosae populations were stressed by crowding, cold, thin phloem, and to drying of the host tissues. A male-lethal factor has been suggested by Lanier

and Wood (1968) as an explanation for highly female-biased broods in Dendroctonus jeffreyi Hopkins.

Alternately, the female-biased sex ratio in progeny from thin phloem could have occurred if I. calligraphus parent females were able to regulate the sex of their progeny. Charnov (1982, p. 65) stated that there are few examples where environmental control of sex development has been documented in diploid insects; haplodiploidy has not been reported in Ips bark beetles (Kirkendall 1983). Another possible explanation for the skewed sex ratio is that there may be more than 1 type of female as reported by Hopping (1962, 1964) and Bakke (1968), for Ips tridens Mannerheim and Ips acuminatus (Gyllenhal), respectively. They reported that some females produce all-female broods while others produce bisexual broods. It is of interest to note that these species occur in northern North America and Europe, respectively, and thus such findings may reflect adaptations by these beetles to their harsh environment. Nevertheless, I have no evidence to support the possibility of 2 types of females in I. calligraphus because in all of my rearing experiments with this bark beetle, I have never observed a single all-female brood. Thus, these latter suggestions probably do not explain the female-biased sex ratio observed in this study when development occurred in thin phloem.

Summary

In summary the following points can be made with respect to *I. calligraphus* development in thin and thick slash pine phloem.

1. The average number of days to 50% re-emergence of parent adults decreases with increasing temperature, but apparently it is unaffected by phloem thickness.
2. The rate of brood development is positively correlated with both temperature and phloem thickness.
3. The number of F1 brood adults produced per parent female increases with both increasing temperature and phloem thickness.
4. The average number of days to 50% emergence of brood adults decreases with both increasing temperature and phloem thickness.
5. Pronotal width of thick-phloem reared brood adults is greater than that of brood adults reared from thin phloem. Male pronotal width is greater than that of females when development occurs in thick phloem but not when it occurs in thin phloem.
6. The sex ratio (male:female) of brood adults is 1:1 when reared in thick phloem and 1:2 when reared in thin phloem.
7. The progeny of thin-phloem reared F1 adults are as large and of the same sex ratio (1:1) as are the

progeny of thick-phloem reared F1 adults when all development occurs in thick phloem.

CHAPTER V
SEASONAL DEVELOPMENT AND DIURNAL ACTIVITY PATTERNS OF IPS CALLIGRAPHUS IN FLORIDA

Introduction

Little information is available on seasonal development of the southern pine bark beetles. Thatcher (1960), extrapolating from developmental rates reported in the literature, predicted that in the southern USA at least 3 generations per year would be completed by Dendroctonus frontalis, and similarly, at least 2 by Dendroctonus terebrans (Olivier), 10 by Ips avulsus, and 6 by both Ips calligraphus and Ips grandicollis. A later study by Thatcher and Pickard (1967) revealed that D. frontalis completed 7 (and a partial 8th) consecutive generations within a year's time in east Texas. Ips calligraphus is reported to complete 4 generations per year in California (Wood and Stark 1968), and 12 generations per year in Mexico (Ascencio 1979).

Many bark and ambrosia beetles show a bimodal pattern of daily flight on warm summer days, with peaks occurring during early morning and again as evening approaches (Anderson 1948; Gara and Vite 1962; Rudinsky 1963; Rudinsky and Daterman 1964; Vite et al. 1964; Hertel et al. 1969).

During the summer in Florida, peak flight of I. calligraphus occurs from 0600-0900 h and 1600-2000 h (Wilkinson 1964). Few records exist on diurnal flight of bark beetles during seasons other than summer. Spring flight often occurs as a single peak during late afternoon (Rudinsky 1963; Rudinsky and Daterman 1964). Kinn (1978) reported that during the winter months in Louisiana, D. frontalis had a single, early afternoon peak of emergence. He also reported similar daily activity patterns for both males and females during the different seasons.

Scolytid flight is influenced greatly by the prevailing weather conditions. Flight activity is generally stimulated by rising temperatures (Henson 1962; Moser and Dell 1979), increasing light intensity (Mason 1969), and with cloudy conditions and the onset of rainstorms (Vite et al. 1964), but retarded by heavy rains (Moser and Dell 1979) and excessive temperatures (Henson 1962). The possible relationship between these meteorlogical phenomena and bark beetle flight behavior has been reviewed by Chapman (1967). For many scolytids in the southern USA, the threshold temperature for flight ranges from 18°-22°C (Vite et al. 1964; Turnbow and Franklin 1980). Predictive equations for D. frontalis developmental time have been established utilizing the day-degree concept of Arnold (1959) and field-collected temperature data (Mizell and Nebeker 1978).

The objectives of this study were (1) to determine the seasonal development (voltinism) of I. calligraphus in thick-phloem slash pines in north-central peninsular Florida, (2) to record the diurnal activity pattern of male and female I. calligraphus adults throughout the year, and (3) to describe the above findings in regard to available weather data for Gainesville, Florida.

Methods and Materials

Tree selection and treatment. Apparently healthy, dominant and co-dominant, 21- to 22-year-old slash pine trees were used in this study. The trees were growing in a plantation with a site index of 58 ft (17.6 m) at 25 years near Orange Heights, Alachua County, Florida. Phloem thickness along the trunk was generally greater than 2.5 mm in all selected trees. Such a thickness was considered "thick" relative to the pronotal width of I. calligraphus adults which generally range from 1.5-2.1 mm in Florida populations (see chapters II and IV). After felling, the trunks were supported off the ground and then left in the field to undergo natural infestation by I. calligraphus and its associates. The trees were inspected every 2-5 days for evidence of bark beetle attack, i.e., pitch tubes and boring frass. During inspection, bark was removed from some attacks along the length of the trunk to determine the beetles' progress. Records were made on presence or absence

of completed nuptial chambers, parent females, eggs, and larvae. Later inspections were made to determine the time of pupation. When most individuals reached the pupal stage, infested trunk sections (50-90 cm long) were cut, returned to the laboratory (a distance of ca. 12 miles), and placed into screen emergence cages (ca. 96 cm long, 71 cm wide, 82 cm high) in an open-air insectary (ca. 5.5 m long, 3.8 m wide, 2.2 m high).

Brood adult collection. Emerging brood adults were collected several times daily from the screen walls of the cages. It was observed that I. calligraphus adults would readily fly and/or walk from the pine logs to the screen walls throughout the day when conditions were presumably favorable for flight. However, when conditions were not favorable, adults were found to remain on the bark of the logs either walking or remaining motionless. Collecting adults from the screen walls was thus considered an appropriate means of approximating the natural diurnal flight activity of I. calligraphus adults. Whenever possible, collections were made at 2-hour intervals from early morning (0700-0900 h) until dusk (1700-2000 h, Eastern Standard Time). Beetles were placed into containers labelled by date and collection time, frozen, sexed according to the form of the third elytral tooth (Hopping 1963), and returned to the freezer and there stored by generation number. Numbers of emerging male and female

brood adults were recorded daily. Average time to 50% brood emergence was calculated when emergence stopped for a given cohort. In addition, length and diameter-inside-bark were recorded for all bolts, and from these values the bark surface area was calculated. The bark was then removed from several of the bolts and the inner surfaces inspected for bark beetles, associates, and extent of cerambycid grazing; observations were recorded.

Generation synchronization. The time at which 50% brood emergence occurred for a given generation was considered the starting point for the subsequent generation. Because the exact day on which 50% emergence was to occur was at first unknown, several trees had to be felled in order to bracket this occasion. This was done by felling 2-6 unifested slash pines throughout the period of brood emergence at 3-7 day intervals (Fig. 5-1). These newly felled trees were inspected regularly as described above for signs of beetle attack with dates and observations recorded. The tree eventually selected as the "brood tree" for the following generation was the one whose date of colonization most closely matched the date of 50% emergence of the then current generation. Overall, one generation was matched to the next with apparently no more than a 1-2 day error. The above procedures were carried out for one generation after another beginning in March 1982 and going through May 1983. The initial generation that developed was used mainly to

develop proper techniques. Then, starting from the date of 50% emergence for that generation, the study was conducted for approximately one year's time.

Data collection and analyses. For each generation, the daily counts of males and females were used to calculate average times to 50% emergence for each sex separately and combined. Means were compared between sexes and among generations using the t-test and Duncan's multiple-range test. Analyses were performed using the general linear models procedures of the Statistical Analysis System (SAS), version 1982.3. Significance was tested at the $P<0.05$ level. The duration of each generation (generation time) was calculated as the number of days between dates of 50% emergence for two consecutive generations. The sex ratio was determined for each generation based on all adults collected. The proportion of males in each generation as well as for all generations combined was compared to 0.5 (the proportion expected in a 1:1 sex ratio) by the z-test (two-tailed) (Freund 1960, p. 253). Similarly, the mean male proportion (averaged over the 9 generations) was compared to 0.5 using the t-test (Freund 1960, p. 222). Brood adult density was calculated for each generation as follows: Brood density = No. adults collected/bark surface area. Data from the numerous daily collections were pooled into 3 convenient diurnal periods: 0700-1000 h (AM), 1100-1400 h (MIDDAY), and 1500-2000 h EST (PM). This was

done because collections could not always be made at the same times from day to day or from generation to generation. The proportion of brood adults that emerged during each of these periods was calculated on a daily basis using only those days on which at least 5 beetles were collected and collections were made at 2-hour intervals from dawn to dusk. Means were compared among generations and the 3 collection periods by Duncan's multiple-range test, after arcsin transformation of the data (Steel and Torrie 1980).

Day-degree accumulation. The day-degree (°D) accumulation for each generation was calculated summing over all days between that generation's date of 50% emergence and that of the generation preceding it. Three lower threshold temperatures and two different methods were used. The temperatures [50° (10.0°C), 55° (12.8°C), and 60°F (15.6°C)] were chosen to bracket the actual developmental threshold temperature of I. calligraphus, which probably lies within these limits. Wilkinson and Foltz (1982) reported a base temperature of about 59°F for I. calligraphus brood development. Based on the 20° and 30°C rearing data presented in chapter IV, the threshold temperature[1] would be

[1] The threshold was calculated as shown by Kapler and Benjamin (1960), where development in relation to temperature is expressed as a constant in the equation K = y(t-a), where "y" is the average number of days required to complete development, "t" is the average daily mean temperature, and "a" is the base temperature. In the above calculations the threshold "a" was calculated by simultaneously solving the equations using the 20° and 30°C rearing data.

about 50.6° (10.3°C) in thin phloem, and 52.5°F (11.4°C) in thick phloem. In the mean-minus-threshold method (Pruess 1983), the formula used was °D = [(MAX° - MIN°)/2] - threshold°; negative values were dropped. In the other method, the above formula was employed when the daily minimum temperature was equal to or greater than the threshold. However, when the daily minimum temperature was below the threshold, the following formula was used: °D = 1/2 [(MAX° - threshold°)²/(MAX° - MIN°)]. The latter formula allows for day-degree accumulation on many days when the mean-minus-threshold method would give negative values (Lindsey and Newman 1956; Arnold 1960). Daily maximum and minimum air temperatures were obtained from the Official Weather Data for Gainesville 3 WSW, Florida.[2] The most appropriate temperature/method combination was selected by comparing their respective coefficients of variation as described by Arnold (1959). This test statistic was generated when the average number of day-degrees per generation was calculated for each of the 6 combinations.

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[2] Published by the Department of Agronomy, University of Florida, Gainesville, Florida 32611, in cooperation with NOAA.

Results

Voltinism, generation time, and brood emergence. *Ips calligraphus* completed 9 consecutive generations during a 1-year period (371 days) in north-central peninsular Florida. Felling dates of brood trees and the overall emergence data are presented in Table 5-1. The period of brood emergence for a single generation ranged from as many as 68 days (Gen. 1) in the winter to as few as 11 days (Gen. 7) in late summer. Similarly, generation time was 81 days in duration for the 2 generations (Gens. 1-2) that developed during the cooler months, and 27-28 days long for the 4 generations (Gens. 4-7) that developed during the warmer months. Percent daily emergence for each of the 9 generations is depicted in Fig. 5-2.

Females tended to emerge before males of the same cohort (Table 5-2). Average number of days to 50% female emergence was significantly less than that of males in each generation. Differences between male and female mean-times to 50% emergence ranged from 8 days for the cohort that emerged during the cooler months (Gen. 1), to 1-2 days for those that emerged during the warmer months (Gens. 4-9). Male and female cumulative percent daily-emergence is presented on a seasonal basis in Fig. 5-3, and in tabular form in Tables 5-3 (winter; Gen. 1), 5-4 (spring; Gen. 2), and 5-5 (summer-fall; Gens. 3-9). These results clearly demonstrate that female emergence was advanced over that of males throughout the entire process of brood emergence.

Sex ratio and brood density. The sex ratio was aproximately 1:1 for 5 generations (Gens. 2,3,5,6,8), but in the other 4 (Gens. 1,4,7,9), the proportion of brood males was significantly different from the theoretical 0.5 (Table 5-2). In addition, the overall male proportion (0.45) of all brood adults (N=7368) was significantly different from 0.5 when tested both as a proportion (z=8.76; two-tailed) and as a mean (t=3.36; df=8; two-tailed).

Brood density varied from over 5 adults/dm² for the generation that developed during the months of April-June (Gen. 3), to fewer than 1 adult/dm² in the generations that developed from January to May (Gen. 2) and from September to October (Gen. 8) (Table 5-2). Brood density declined from generation to generation throughout the summer (Gens. 3-7).

Diurnal and seasonal activity patterns. In general, the diurnal activity pattern of males and females did not differ significantly within any generation. The data were thus pooled with respect to sex. Similarly, the diurnal activity pattern did not differ significantly among generations 4-7, and thus these data were pooled. Consistent data with respect to collection time were not available for generations 3 (collection times had not yet been standardized) and 9 (because the author was hospitalized).

The pattern of daily activity shifted from season to season (Table 5-6). In spring (Gen. 2), two-thirds of the adults were collected during the PM, with fewer recovered

near MIDDAY, and the fewest during the AM. As the spring days became warmer, beetles were collected progressively earlier during the day; beetles emerging in spring were first collected at 1000 h on 8 May and at 0800 h on 16 May 1983. During the summer (Gens. 4-7), adult activity was greatest in the PM, with the next most active period being the AM. On several summer days no beetles were collected during the MIDDAY period. In fall (Gen. 8), beetles were most active during the MIDDAY and PM periods. During winter (Gen. 1), nearly three-fourths of the adults were recovered near MIDDAY, and of those remaining, most were collected at PM. Adults were collected only once during the AM (at 1000 h on 30 January 1983) in winter. That day was unseasonably warm for Gainesville; maximum and minimum air temperatures were 78° and 50°F (25.6° and 10.0°C), respectively, compared to the January 1983 monthly average of 65.2° and 42°F (18.4° and 5.6°C). No beetles were collected later in the day than 1600 h until 6 March 1983, when some were recovered at 1700 h. With respect to the three collection periods, beetle activity was greatest in the AM during summer, at MIDDAY during winter, and in the PM during spring (Table 5-6).

Day-degree accumulation. Day-degree summations for each of the 9 generations were quite similar (Table 5-7). There was generally best agreement among the summer generations (Gens. 3-8), regardless of the threshold temperature used. However, for generations 1 and 9, fewer heat units were

accumulated when 55° and 60°F were used as threshold temperatures. The smallest coefficient of variation (CV) was associated with a threshold temperature of 50°F and the mean-minus-threshold method, suggesting that this combination is the most appropriate of those tested.

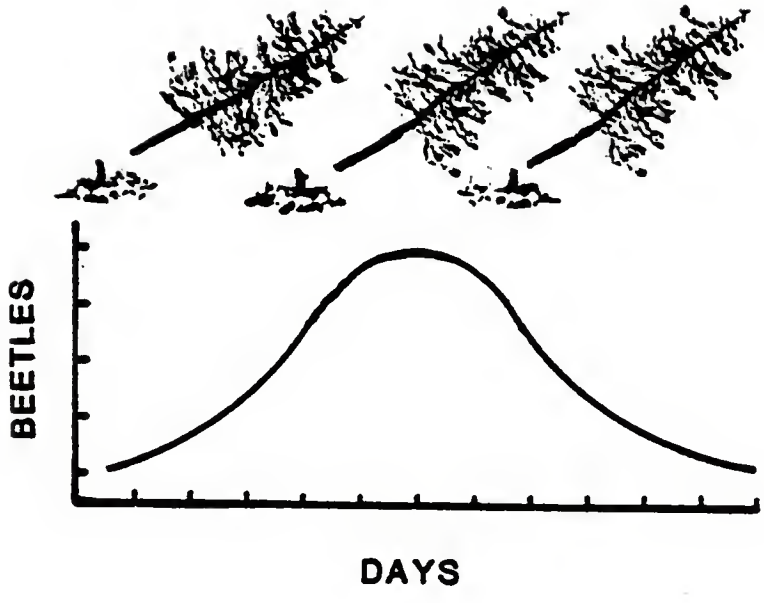

Fig. 5-1. Schematic representation of the field methods employed in the Ips calligraphus voltinism study. Depicted are (1) emergence of brood adults for a given generation through time and (2) the felling of thick-phloem pine trees on various days throughout this period of brood emergence, which were then allowed to undergo natural infestation. The tree felled and infested nearest to the time of 50% brood emergence was selected as the "brood" tree for the following generation.

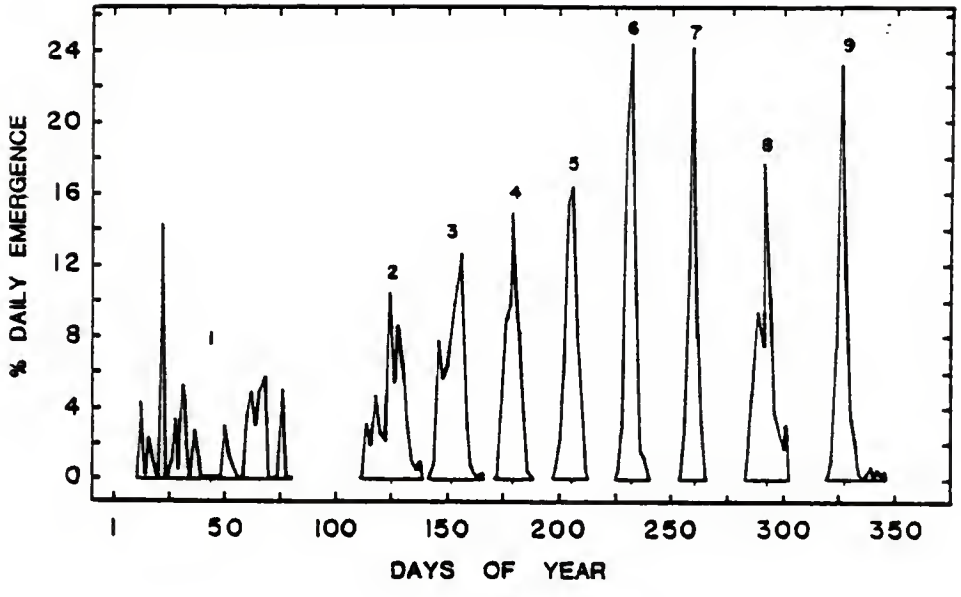

Fig. 5-2. Percent daily emergence (on a per-generation basis) of Ips calligraphus brood adults during each of 9 generations that were completed during a 1-year period (May 1982-May 1983) near Gainesville, Florida. Beetles were reared from slash pines with relatively thick phloem.

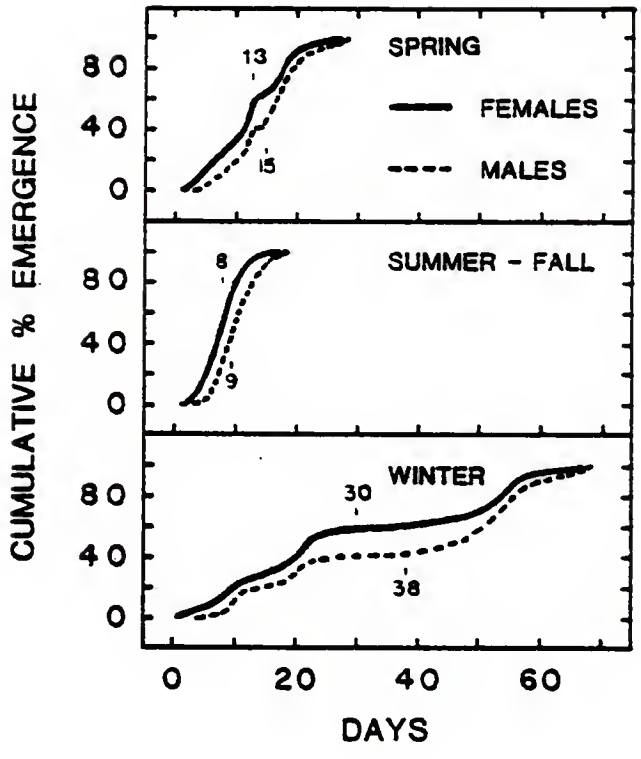

Fig. 5-3. Cumulative emergence for male and female Ips calligraphus brood adults that emerged during spring (generation 2), summer-fall (generations 3-9), and winter (generation 1) of the year May 1982 - May 1983 near Gainesville, Florida. Beetles were reared from slash pines with relatively thick phloem. The number on each curve represents the average number of days from first emergence for a given cohort to the time of 50% brood emergence.

Table 5-1. Summary data for the Ips calligraphus voltinism study including for each generation (Gen) the tree felling date; the first, last and total number of days of brood emergence; the average number of days to 50% brood emergence and the date on which it occurred; and the number of days between the date of 50% emergence for a given generation and that of the generation preceding it (Gen. Time).

		Brood Emergence (Days)					
		Dates			50% Emergence[1]		
Gen	Felling Date	First	Last	No.	$\bar{X} \pm$ SD[2]	Date	Gen. Time
1	17 NOV 82	11 JAN	19 MAR	68	33.2 ± 20.4a	12 FEB	81
2	9 JAN 83	21 APR	19 MAY	29	14.0 ± 5.8b	4 MAY	81
3	23 APR 82	22 MAY	13 JUN	23	10.2 ± 3.5c	31 MAY	33[3]
4	22 MAY 82	20 JUN	6 JUL	17	8.0 ± 3.0de	27 JUN	27
5	23 JUN 82	17 JUL	3 AUG	16	8.1 ± 2.7d	24 JUL	27
6	21 JUL 82	14 AUG	28 AUG	15	7.1 ± 2.1e	20 AUG	27
7	18 AUG 82	11 SEP	21 SEP	11	7.1 ± 1.7e	17 SEP	28
8	13 SEP 82	11 OCT	28 OCT	18	8.7 ± 4.0d	19 OCT	32
9	14 OCT 82	16 NOV	11 DEC	26	8.1 ± 3.2de	23 NOV	35

[1]Mean times to 50% emergence were based on the emergence data from all brood adults collected for a given generation, starting from the day of first emergence for that generation.

[2]Means followed by the same letter are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

[3]Gen. time for generation 3 was calculated starting from the date of 50% emergence (28 April 1982) for the cohort that developed in the initial tree cut on 19 March 1982.

Table 5-2. Average number of days to 50% emergence of Ips calligraphus male and female brood adults (starting from the first day of emergence for each individual generation), the brood adult sex ratio (%), and brood density (brood adults/dm² of bark; F1/dm²), by generation (Gen).

Gen	N[1]	Days to 50% Emergence: Male $\bar{X} \pm SD$[2]	Days to 50% Emergence: Female $\bar{X} \pm SD$	Sex Ratio (%): M[3]	Sex Ratio (%): F	Brood Density[4]: dm²	Brood Density[4]: F1/dm²
1	427	38.2±20.3a1	29.9±19.8a2	40*	60	282	1.5
2	381	15.3± 5.5b1	12.9± 5.9b2	45	55	452	0.8
3	2170	10.4± 3.6c1	10.2± 3.4c2	48	52	424	5.1
4	1720	8.7± 2.9de1	7.4± 2.9d2	42*	58	493	3.5
5	750	8.7± 2.5de1	7.7± 2.7d2	47	53	225	3.3
6	591	7.7± 2.0e1	6.6± 2.0d2	49	51	253	2.3
7	551	7.7± 1.4e1	6.6± 1.8d2	41*	59	250	2.2
8	258	9.5± 3.7cd1	7.6± 4.0d2	52	48	381	0.7
9	520	8.7± 3.0de1	7.7± 3.3d2	39*	61	330	1.6

[1] N=number of brood adults collected for each generation.

[2] Means followed by the letter (within columns) on number (Within rows) are not significantly different at the $P<0.05$ level (Duncan's multiple-range test).

[3] Values followed by an "*" are significantly different from 0.5 when tested as a proportion (z-test; two-tailed).

[4] Brood density was calculated as follows: F1/dm² = No. of F1 adults collected/total surface area in dm².

Table 5-3. Daily emergence for Ips calligraphus male (N=169) and female (N=258) brood adults that emerged during the "winter" (generation 1) of 1983 near Gainesville, Florida.

	Winter Emergence								
	Male			Female			Males + Females		
Day[1]	N	%	Cum.%	N	%	Cum.%	N	%	Cum.%
1	3	1.8	1.8	15	5.8	5.8	18	4.2	4.2
3	0			1	0.4	6.2	1	0.2	4.4
5	3	1.8	3.6	6	2.3	8.5	9	2.1	6.6
7	0			2	0.8	9.3	2	0.5	7.0
8	0			2	0.8	10.1	2	0.5	7.5
11	22	13.0	16.6	39	15.1	25.2	61	14.3	21.8
12	7	4.1	20.7	7	2.7	27.9	14	3.3	25.1
14	0			2	0.8	28.7	2	0.5	25.6
15	2	1.2	21.9	2	0.8	29.5	4	1.0	26.5
17	2	1.2	23.1	12	4.7	34.1	14	3.3	29.7
18	0			3	1.2	35.3	3	0.7	30.4
19	5	3.0	26.0	9	3.5	38.8	14	3.3	33.7
20	8	4.7	30.8	15	5.8	44.6	23	5.4	39.1
21	7	4.1	34.9	13	5.0	49.6	20	4.7	43.8
22	5	3.0	37.9	11	4.3	53.9	16	3.7	47.5
25	0			1	0.4	54.3	1	0.2	47.8
26	3	1.8	39.6	10	3.9	58.1	13	3.0	50.8
27	0			5	1.9	60.1	5	1.2	52.0
28	1	0.6	40.2	1	0.4	60.5	2	0.5	52.5
36	0			1	0.4	60.9	1	0.2	52.7
39	6	3.6	43.8	7	2.7	63.6	13	3.0	55.7
41	2	1.2	45.0	4	1.6	65.1	6	1.4	57.1
43	1	0.6	45.6	1	0.4	65.5	2	0.5	57.6
44	5	3.0	48.5	1	0.4	65.9	6	1.4	59.0
46	3	1.8	50.3	3	1.2	67.1	6	1.4	60.4
48	2	1.2	51.5	1	0.4	67.4	3	0.7	61.1
49	9	5.3	56.8	6	2.3	69.8	15	3.5	64.6
51	9	5.3	62.1	12	4.7	74.4	21	4.9	69.6
52	3	1.8	63.9	8	3.1	77.5	11	2.6	72.1
53	8	4.7	68.6	5	1.9	79.5	13	3.0	75.2
54	11	6.5	75.1	14	5.4	84.9	25	5.9	81.0
55	9	5.3	80.5	12	4.7	89.5	21	4.9	85.9
57	11	6.5	87.0	13	5.0	94.6	24	5.6	91.6
58	2	1.2	88.2	4	1.6	96.1	6	1.4	93.0
65	16	9.3	97.6	6	2.3	98.5	22	5.2	98.1
66	3	1.8	99.4	1	0.4	98.8	4	1.0	99.1
68	1	0.6	100.0	3	1.2	100.0	4	1.0	100.0

[1]Data are presented for only those days on which brood adults were collected, with "day 1" representing the first day of emergence.

Table 5-4. Daily emergence for Ips calligraphus male (N=173) and female (N=208) brood adults that emerged during the "spring" (generation 2) of 1983 near Gainesville, Florida.

	Spring Emergence								
	Male			Female			Males + Females		
Day[1]	N	%	Cum.%	N	%	Cum.%	N	%	Cum.%
1	0			1	0.5	0.5	1	0.3	0.3
2	0			2	0.9	1.4	2	0.5	0.8
3	3	1.7	1.7	9	4.3	5.8	12	3.1	3.9
4	1	0.6	2.3	8	3.8	9.6	9	2.4	6.3
5	3	1.7	4.0	6	2.9	12.5	9	2.4	8.7
6	5	2.9	6.9	10	4.8	17.3	15	3.9	12.6
7	4	2.3	9.2	14	6.7	24.0	18	4.7	17.3
8	6	3.5	12.7	5	2.4	26.4	11	2.9	20.2
9	6	3.5	16.2	4	1.9	28.4	10	2.6	22.8
10	8	4.6	20.8	11	5.3	33.7	19	5.0	27.8
11	4	2.3	23.1	5	2.4	36.1	9	2.4	30.2
12	15	8.7	31.8	24	11.5	47.6	39	10.2	40.4
13	14	8.1	39.9	26	12.5	60.1	40	10.5	50.9
14	1	0.6	40.5	1	0.5	60.6	2	0.5	51.4
15	12	6.9	47.4	10	4.8	65.4	22	5.8	57.2
16	10	5.8	53.2	3	1.4	66.8	13	3.4	60.6
17	22	12.7	65.9	10	4.8	71.6	32	8.4	69.0
18	11	6.4	72.3	22	10.6	82.2	33	8.7	77.7
19	12	6.9	79.2	12	5.8	88.0	24	6.3	84.5
20	8	4.6	83.8	8	3.8	91.8	16	4.2	88.2
21	8	4.6	88.4	3	1.4	93.3	11	2.9	91.1
22	6	3.5	91.9	5	2.4	95.7	11	2.9	94.0
23	1	0.6	92.5	3	1.4	97.1	4	1.0	95.0
24	5	2.9	95.4	2	1.0	98.1	7	1.8	96.8
25	2	1.2	96.5	0			2	0.5	97.4
26	0			3	1.4	99.5	3	0.8	98.2
27	3	1.7	98.3	1	0.5	100.0	4	1.0	99.2
28	9	1.2	99.4				2	0.5	99.7
29	1	0.6	100.0				1	0.3	100.0

[1]Data are presented for only those days on which brood adults were collected, with "day 1" representing the first day of emergence.

Table 5-5. Daily emergence for Ips calligraphus male (N=2967) and female (N=3593) brood adults that emerged during the "summer" and "fall" of 1982 (generations 3-9) near Gainesville, Florida.

	Summer and Fall Emergence								
	Male			Female			Males + Females		
Day[1]	N	%	Cum.%	N	%	Cum.%	N	%	Cum.%
1	2	0.1	0.1	20	0.6	0.6	22	0.3	0.3
2	20	0.7	0.7	55	1.5	2.1	75	1.1	1.5
3	31	1.0	1.8	111	3.1	5.1	142	2.2	3.6
4	87	2.9	4.7	250	7.0	12.1	337	5.1	8.8
5	197	6.6	11.4	374	10.4	22.5	571	8.7	17.5
6	263	8.9	20.2	405	11.3	33.8	668	10.2	27.7
7	373	12.6	32.8	449	12.5	46.3	822	12.5	40.2
8	370	12.5	45.3	356	9.9	56.2	726	11.1	51.3
9	387	13.0	58.3	448	12.5	68.7	835	12.7	64.0
10	289	9.7	68.0	322	9.0	77.7	611	9.3	73.3
11	252	8.5	76.5	223	6.2	83.9	475	7.2	80.5
12	210	7.1	83.6	187	5.2	89.1	397	6.2	86.6
13	212	7.1	90.8	178	5.0	94.0	390	5.9	92.5
14	129	4.3	95.1	103	2.9	96.9	232	3.5	96.1
15	70	2.4	97.5	47	1.3	98.2	117	1.8	97.9
16	35	1.2	98.7	23	0.6	98.8	58	0.9	98.8
17	12	0.4	99.1	9	0.3	99.1	21	0.3	99.1
18	13	0.4	99.5	8	0.2	99.3	21	0.3	99.4
19	3	0.1	99.6	4	0.1	99.4	7	0.1	99.5
20	6	0.2	99.8	11	0.3	99.7	17	0.3	99.8
21	1	0.03	99.8	0			1	0.01	99.8
22	3	0.1	99.9	0			3	0.05	99.8
23	1	0.03	99.97	8	0.2	99.94	9	0.1	99.9
25	0			1	0.03	99.97	1	0.01	99.9
26	1	0.03	100.0	1	0.03	100.0	2	0.03	100.0

[1]Data are presented for only those days on which brood adults were collected, with "day 1" representing the first day of emergence for each individual generation.

Table 5-6. Mean (%) Ips calligraphus brood adult emergence during three daily periods per-day by season from May 1982 to May 1983 near Gainesville, Florida.

	Daily Emergence Periods (EST)		
	0700-1000 h	1100-1400 h	1500-2000 h
N[1]	$\bar{X} \pm SD$[2] (Range)	$\bar{X} \pm SD$ (Range)	$\bar{X} \pm SD$ (Range)
Winter (Gen. 1)			
277	1.6 ± 5.8c3 (0 - 22)	75.8 ± 17.0a1 (43 - 100)	22.4 ± 17.4c2 (0 - 57)
Spring (Gen. 2)			
321	6.4 ± 11.2bc3 (0 - 36)	29.4 ± 19.7bc2 (0 - 83)	64.2 ± 18.5a1 (17 - 87)
Summer (Gens. 4-7)			
2819	35.5 ± 2.7a2 (14 - 62)	13.6 ± 10.7c3 (0 - 47)	51.4 ± 15.1b1 (14 - 80)
Fall (Gen. 8)			
145	13.8 ± 16.1b2 (0 - 44)	36.3 ± 13.2b1 (19 - 59)	50.0 ± 8.3b1 (38 - 58)

[1]N=total number of beetles that emerged during each season when at least 5 beetles emerged on a given day and collections were made every 2 hours throughout the day: 14 days in winter, 15 days in spring, 26 days in summer, and 7 days in fall.

[2]Means followed by the same letter (within columns) or number (within rows) are not significantly different at the $P < 0.05$ level (Duncan's multiple-range test).

Table 5-7. Day-degree summations above 50°, 55°, and 60°F using the Lindsey and Newman (L&N) and the mean-minus-threshold (M-T) methods for each of the 9 generations (Gen) that Ips calligraphus completed in a 1-year period near Gainesville, Florida. Additionally, the mean, standard deviation (SD), and coefficient of variation (CV) are presented for each temperature-method combination.

Gen	Summation Period[1] Calendar Dates	Days	Day-degree Summations[2] 50°F L&N[3]	50°F M-T[4]	55°F L&N	55°F M-T	60°F L&N	60°F M-T
1	24 NOV 82-12 FEB 83	81	882	803	591	536	360	320
2	13 FEB 83- 4 MAY 83	81	1071	1024	743	667	468	366
3	29 APR 82-31 MAY 82	33	802	802	637	637	476	475
4	1 JUN 82-27 JUN 82	27	803	803	668	668	475	475
5	28 JUN 82-24 JUL 82	27	847	847	712	712	577	577
6	25 JUL 82-20 AUG 82	27	835	835	700	700	565	565
7	21 AUG 82-17 SEP 82	28	869	869	729	729	589	589
8	18 SEP 82-19 OCT 82	32	804	804	645	644	587	484
9	20 OCT 82-23 NOV 82	35	619	612	459	441	311	288
Mean			837	822	654	637	485	466
SD			117	106	88	93	96	115
CV			13.9	12.9	13.4	14.5	19.8	24.6

[1]Summation periods were defined as follows: from the first day following the date of 50% brood emergence of the preceding generation to the date of 50% emrgence for the generation being considered.

[2]Temperature data were based on the Official Weather Data for Gainesville, Florida 3 WSW, published by the University of Florida and NOAA.

[3]L&N=[(MAX°-Threshold°)²/(MAX°-MIN°)]/2 when the minimum daily temperature was below the threshold, otherwise, the M-T method was used as given below.

[4]M-T=[(MAX°+MIN°)/]-Threshold°, with negative values dropped.

Discussion

Seasonal development. Overall, the temperatures experienced in Gainesville, Florida, during the time of this study were very similar to the area's 70-year average. The day-degree summations, using the mean-minus-base method and 50°F as base, were 7399°D during the year of the study and 7360°D based on the 70-year average. Therefore, the fact that I. calligraphus completed 9 generations during the course of a single year is probably quite representative for the Gainesville area. Using 837°D above 50°F as the heat unit requirement for one generation of I. calligraphus and the U.S. Weather Bureau 40-year-average temperature data for Florida (U.S. Department of Commerce 1964), 8.8 generations/year are predicted for I. calligraphus near Gainesville, Florida. In Florida, the range of slash pine (both varieties) extends from the northern counties southward to the Florida Keys (Critchfield and Little 1966). Considering the same temperature requirements for I. calligraphus development throughout Florida, from as few as 7.3 generations/year would occur near Niceville in northwestern Florida, to as many as 12.1 near Key West, Florida, on the average.

Nevertheless, it should be recognized that only trees with relatively thick (2.5-3.5 mm) phloem were used in this study. It is in such material that I. calligraphus develops relatively fast (chapter IV). Therefore, 9 generations per

year is probably an appropriate value for I. calligraphus in slash pine plantations where average phloem thickness is thick, but an overestimate where it is thin (0.5-1.5 mm). It was noted in chapter IV that average time to 50% brood emergence from thin phloem generally followed that of thick phloem by 3-5 days. A similar observation was documented in the field. A thin-phloem tree was felled on the same day as was the thick-phloem tree used as the brood tree for generation 2; time of colonization was also similar for the 2 trees. Average time to 50% brood emergence occurred 5 days later for the thin-phloem tree. Therefore, if developmental time for each generation was extended by 3-5 days, over a year's time only 7-8 generations would probably be completed in thin phloem near Gainesville, Florida.

Male and female emergence. The fact that, on the average, females emerged sooner than males indicates that males may develop slower or over a longer period of time than do females. Dale (1967) noted earlier emergence by I. calligraphus females in several of his rearing studies. A longer developmental time for males may be the proximate mechanism by which males achieve a larger body size compared to females (Dale 1967; chapters II and IV). Such dimorphism would be of considerable importance because it is the male that initiates attack; several advantages to males being larger than females were postulated in chapter IV. In D. frontalis, the female initiates attack and is the larger of the sexes (Hedden and Billings 1977).

Assuming that little or no mating occurs prior to emergence among I. calligraphus siblings, earlier emergence by females could lead to greater outcrossing, and thus higher levels of heterozygosity would be maintained among field populations. Under most conditions, heterozygotes have greater survival value than either homozygous type (Dobzhansky 1951). There is probably little risk of a female emerging too early and not finding a mate because I. calligraphus generations overlap extensively and thus males are present throughout the year. It should be mentioned, however, that pre-emergence mating among siblings has been recorded for I. grandicollis (Witanachchi 1980). In other bark beetles, the sex found to predominate early stages of emergence is usually not the one which initiates attack on the new host: females in Ips paraconfusus Lanier (Cameron and Borden 1967) and males in Dendroctonus ponderosae (Billings and Gara 1975).

Sex ratio. The sex ratio (males:females) of I. calligraphus brood adults is generally 1:1 (Wray 1951; Dale 1967; Cook et al 1983). I reported in chapter IV that the sex ratio of brood adults was 1:1 when reared from thick phloem and 1:2 when reared from thin phloem. Why then, if all trees in the present study had thick phloem, were there significantly fewer males than females in 4 of the 9 generations, as well as fewer males overall? If developmental time is truly longer for males, then perhaps

males would be subject to higher rates of (1) cannibalism, (2) parasitism and predation, and (3) interspecific competition by cerambycids and other "phloem-grazers." Coulson et al. (1976, 1980) described the competitive interactions between the cerambycid, Monochamus titillator (Fabricius), and D. frontalis. The 1:1 sex ratio reported in my laboratory studies involving thick phloem (chapter IV) may have resulted because of the absence of these natural mortality agents. Intraspecific competition in these laboratory studies (chapter IV) would probably also have been less, considering the low initial stocking densities of parent adults used. The lower proportions of males during the cooler months (Gens. 1 and 9) may reflect greater susceptibility of males to cold, desiccation, and/or changes in food quality. Lower male survival in D. ponderosae is related to length of exposure to cold (Watson 1971; Safranyik 1976), and to drying (Cole et al. 1976).

Brood density. The gradual decline in brood density throughout the summer suggests that biotic factors may account for progressively greater mortality as the season progresses. This of course assumes similar attack densities and oviposition rates throughout the summer. Because all trees were felled within 100 m of each other, the observed variations cannot be explained on the basis of site to site differences. In late spring and early summer, daily high temperatures in the Gainesville area jumped from the low

80's to the low 90's°F (ca. 27° and 32°C). It was the generation developing during this time that had the greatest brood density (Gen. 3). Perhaps I. calligraphus is able to take advantage of these warmer temperatures faster than can its associates, and thereby suffers less mortality. Goyer and Finger (1980) reported that hymenopterous parasites of D. frontalis were most abundant from June to August in Louisiana. Associates of I. calligraphus, including cerambycids, predators and parasites, became visually more abundant as the summer progressed. Cerambycid grazing was very extensive in the generation 8 rearing material, possibly explaining why brood density in this generation was the lowest of all. The relatively low densities recorded during the winter months may have resulted from exposure to lethal low temperatures; below-freezing temperatures were recorded on 7 nights. Desiccation of the rearing materials may be another factor; the time from date of felling to date of last emergence, was 122 and 130 days for generations 1 and 2, respectively. No doubt changes in food quality also occurred during these long periods of time. The beetles could also be affected indirectly if their symbiotic yeasts and fungi did not develop normally under winter conditions.

Diurnal activity patterns. Although the diurnal activity patterns of I. calligraphus were based on collections in an insectary, the results do agree with those of field studies reported in the literature. The bimodal summertime activity

observed by Wilkinson (1964) and Vite et al (1964), was recorded again in this study. The single peak of late-afternoon activity during spring and fall, and the midday peak during winter, that had previously been described for other scolytids has now been documented for I. calligraphus.

In Texas, I. calligraphus was not observed to fly when temperatures exceeded 86°F (30°C) (Vite et al. 1964). In Florida, summertime temperatures at midday usually exceed that upper limit, and thus may contribute to the midday decline in adult activity. But this midday reduction in beetle activity may not be solely a temperature-dependent response as discussed by Chapman (1967). He argues that the bimodal pattern often observed on warm days is related primarily to "odour meteorology." That is, in early morning and late afternoon the air is relatively stable, allowing pheromone plumes to extend horizontally. Whereas by midday, the air has become unstable with pheromones moving erratically as the air moves upward in strong convective currents. Thus, beetle activity is greatest at those times when pheromone plumes can be tracked most easily, and least when tracking becomes most difficult. The clerid, Thanasimus dubius (Fabricius), is a predator of bark beetles and apparently uses the bark beetle pheromones in locating them (Vite et al. 1964). It is of interest that T. dubius also demonstrates bimodal activity during the summer (Dix and Franklin 1977).

Activity of I. calligraphus adults is affected by atmospheric phenomena. In summer, few beetles were ever collected on windy days or during heavy rains. Beetle activity usually occurred earlier in the afternoon when cloudy. According to Chapman's (1967) hypothesis, such behavior could be related to the convective currents being less intense under cloudy conditions; therefore, pheromones would be more easily tracked. Similar observations were made for D. frontalis by Vite et al. (1964) and Moser and Dell (1979).

In wintertime, however, adult activity appears to be strongly temperature dependent. Vite et al. (1964) did not observe I. calligraphus flight when temperatures were below 68°F (20°C). During emergence of generation-1 adults, the average daily maximum temperature was 68°F on days (N=24) when at least 5 beetles were collected, and less than 63°F (17°C) on days (N=25) when no beetles were collected. Thus, it is not surprising that I. calligraphus activity peaks at midday when temperatures are warmest during the cooler months of the year. This sporadic pattern of emergence during generation 1 is clearly indicated in Fig. 5-2. To the north of Florida, in the Georgia Piedmont, scolytids do not fly during the months of December and January (Turnbow and Franklin 1980). However, in Louisiana (Kinn 1980), North Carolina (McClelland and Hain 1979), and Texas (Thatcher 1967), D. frontalis emergence has been recorded on warmer days during the winter.

Day-degree accumulation. The good agreement among the day-degree summations for the 9 generations is rather remarkable considering that (1) it is not known if the 9 generations were matched end-to-end exactly, (2) brood development occurred first within a forest stand and later in an open-air insectary, and (3) the weather data were recorded at the University of Florida Agronomy Farm. Conversely, it could be argued that the general agreement among the day-degree summations indicates that the field methods were sound; that is, if we consider I. calligraphus to have a given developmental threshold temperature, then the periods of time referred to as "generation times" should split the year into equal heat-unit parcels. The fact that this roughly occurred gives credibility to the study's methods and findings.

Two interesting points arise with reference to the summation values presented in Table 5-7. The first is the relatively low day-degree summations for generations 1 (at 55° and 60°F) and 9 (at 50°, 55°, and 60°F). For sake of discussion, consider the summations to accurately describe the conditions under which these two cohorts developed. One possible explanation for these low values is that I. calligraphus cohorts develop at a lower threshold temperature during the cooler portions of the year. Such would be advantageous to the insect in allowing it to continue development when temperatures are relatively low.

As an example, consider 60°F to be the threshold for the summertime generations (Gens. 2-8), and 55°F to serve as the threshold during for the winter generations (Gens. 1 and 9). Doing this, an inspection of Table 5-7 shows more overall agreement among generations. Nevertheless, the author knows of no instances where a multivoltine insect changes its developmental threshold from season to season. However, Campbell et al. (1974) reported that Canadian populations of certain aphid species had lower threshold temperatures than did Californian populations of those same species.

The second point pertains to the relatively large number of day-degrees that were summed during development of generation 2, when 50°F is used as the threshold temperature. This large sum may reflect protracted development as a result of (1) the larvae being weakened by freezing temperatures, (2) desiccation of the rearing materials, and/or (3) lowering of the food quality with time. Subfreezing temperatures have been shown to cause greater mortality in D. frontalis (McClelland and Hain 1979). Low moisture content in wood is related to protracted development of the cerambycid, Hylotrupes bajulus (Cannon and Robinson 1981).

It is of interest to follow the history of colonization of the brood tree used in generation 2. Although felled on 9 January 1983, attacks were first observed on 30 January 1983; the slow drying of the phloem may have prevented

successful colonization during that period of time. By 2 February, after 4 days of warm weather (daily highs were 77°-80°F; ca. 25°-27°C), attacks (boring frass) were observed along the length of the tree. Several nuptial chambers were fully constructed by this date. Females were found in a few nuptial chambers, and some had laid 1-5 eggs. From 3-17 February, temperatures were cool (daily highs were 55°-69°F, mean=64°F; ca. 13°-21°C, 18°C), and little additional colonization as well as oviposition took place. During the next 3 weeks (18 February-10 March), temperatures were considerably warmer (daily highs were 68°-85°F, mean=75°F; ca. 20°-29°C, 24°C). Colonization by both males and females continued during this warmer period of time. Four days of cooler temperatures then followed, with average highs of 61.5°F (16°C) and lows of 35°F (2°C). This lengthy period of colonization with intermittent cold spells would have allowed for some day-degree accumulation above the selected thresholds, but with probably little concomitant oviposition and brood development. Studies on the threshold temperature for I. calligraphus oviposition are lacking.

Time of 50% brood emergence from the tree felled 19 March 1982 occurred on 28 April 1982, for a generation time of no more than 40 days; first and last day of emergence were 19 April and 20 May, respectively. This is less than half the time required for complete development of generation 2 (81 days; 13 February-4 May 1983). In 1982, the day-degree

accumulation from 20 March-28 April was 765°D, using a base of 50°F and the mean-minus-base method. Such comparisons suggest that wintertime colonization, reproduction, and development are subject to many stressful conditions resulting in prolonged generation time. Also, such information demonstrates the importance of the starting date for voltinism studies of multivoltine insects such as I. calligraphus. That is, had 20 March 1982 been taken as the starting date for this study, then 9 and a partial 10th generation would have been completed by 19 March 1983. Whereas using 29 April 1982 as the starting date, 8 and a partial 9th generation were completed by 28 April 1983.

Summary

In summary, the following points can be made in reference to I. calligraphus development in slash pine trees with thick phloem near Gainesville, Florida.

1. Ips calligraphus completes about 9 generations per year in north-central peninsular Florida.
2. Nearly three months are required to complete one generation during the cooler months, but less than one month is needed in summer.
3. On the average, female brood adults emerge sooner than do males of the same cohort.
4. The sex ratio of brood adults is slightly female-biased, being about 55% females.

5. Density of emerging brood adults declines from generation to generation throughout the summer months and remains relatively low during the winter months.
6. The diurnal activity patterns of adult males and females are similar from season to season.
7. Adults are most active during early morning and evening hours in summer, during late afternoon in spring and fall, and near midday in winter.
8. The emergence threshold of I. calligraphus is apparently between 64°-66°F (18°-19°C).
9. The mean-minus-threshold method of day-degree estimation using 50°F as threshold provides rather consistent summations for I. calligraphus generations times.
10. Using the above method and threshold temperature, an average of 837°D are accumulated per generation.

CHAPTER VI
FIELD STUDIES ON SPATIAL ATTACK PATTERN, REPRODUCTION, AND BROOD DEVELOPMENT OF IPS CALLIGRAPHUS IN RELATION TO SLASH PINE PHLOEM THICKNESS

Introduction

Results of the laboratory studies discussed in chapters II-IV demonstrated that a significant relationship existed between slash pine phloem thickness and Ips calligraphus adult reproduction, as well as brood adult time to 50% emergence, sex ratio, and body size (as measured by pronotal width). However, such studies were conducted under controlled laboratory conditions, using standard densities of artificially introduced parent adults. It was thus logically asked if the above effects would be confirmed when I. calligraphus adults were allowed to colonize host materials with different phloem thicknesses in the field. Under such natural conditions, parent males would be able to establish their own spatial pattern of attack and variable numbers of females could join a given male; thus, natural restraints would be placed on subsequent larval intraspecific competition. Additionally, parent adults and their progeny would interact with the complex of biotic and abiotic factors present in the natural world.

Therefore, studies were conducted under experimental field conditions to determine if phloem thickness had a significant effect on the following population parameters: (1) the spatial attack pattern (based on nuptial chamber distribution); (2) attack density (nuptial chambers/dm^2); (3) harem size (parent females/parent male); (4) gallery density (cm/dm^2); (5) egg density ($eggs/dm^2$); (6) time to 50% brood adult emergence; (7) brood density (brood $adults/dm^2$); (8) egg-to-adult brood mortality; (9) brood adult sex ratio; and (10) brood adult body size (pronotal width in millimeters).

Methods and Materials

Tree selection

This experiment was conducted in two parts with the replicates separated in time by about 10 days during late summer and fall of 1982. In the first replicate (Rep. 1), 2 slash pines with thick (3-4 mm) phloem and 2 with thin (1-2 mm) phloem were felled on 26 August. Another set of 4 trees for Rep. 2 was felled on 6 September. All 8 trees were 21-years-old and growing in a plantation with a site index of 58 ft (17.6 m) at 25 years, near Orange Heights, Alachua County, Florida. Tree diameters (outside bark) at breast height (1.4 m) were 20, 21, 22, and 25 cm for the thick-phloem trees, and 17, 19, 19, and 21 cm for the thin-phloem trees.

Bolt preparation

After felling, 5 bolts (55 cm long; ca. 12-17 cm diam. inside bark) were cut from the trunk of each tree and transported to the laboratory (5 bolts/tree x 8 trees = 40 bolts). An attempt was made to select only those bolts that were similar both in diameter and outer-bark topography. In order to accomplish this, bolts were taken from mostly the lower two-thirds of the main trunk on thin-phloem trees, and from mostly the upper two-thirds on thick-phloem trees. An estimate of each bolt's average phloem thickness was made from 8 samples; 4 were taken from near the top and 4 near the bottom of each bolt. Following drying at 40°C and 40-50%RH for 3-4 days, the bolt ends were pared back to unstained phloem and then dipped successively in a benomyl fungicide-water solution (1%) and melted paraffin to inhibit contamination and desiccation. A screw hook was inserted into the center of each bolt's upper surface and then all bolts were stored at 25°C until used.

Male introduction into bolts

Two adult males were artificially introduced into each bolt ("introduced" males) prior to bolt placement in the field. This was done to ensure rapid colonization of the bolts by way of male pheromone production and thus increasing the area's relative attractiveness to "wild" populations of I. calligraphus and associates (Wilkinson

1964; Renwick and Vite 1972). The introduced males were reared from 2 naturally-infested slash pine trees. Adults were collected daily, sexed according to the form of the third elytral tooth (Hopping 1963), placed into cartons with moist paper towels and stored at 20°C until used. Only males collected within 3 days of the time of introduction were used.

Males were introduced following the methods of Wilkinson (1964). Two "starter holes" were drilled through the outer bark and into the underlying phloem on opposite sides of each bolt halfway between ends. Care was taken to locate each starter hole at the base of a natural bark crevice. A single adult male was placed into the long section of a size 00 gelatin capsule that had been pierced on the end for ventilation and contained a ring of paper for footing. The capsule was secured over the starter hole with a ring of Duxseal(R) sealing compound. Males not actively boring within 1 h after introduction were replaced. Males were allowed 24 h at 25°C to construct a nuptial chamber before placement in the field. Males were introduced on 30 August in Rep. 1 and on 9 September in Rep. 2.

Exposure of bolts on turntables

The infested bolts were transported to the "Honey Plant" on the south side of Gainesville, Alachua County, Florida and suspended from "turntables." The turntables were

located beneath an oak canopy with much of the surrounding area planted to pine or in pasture. A turntable consisted of one movable disc with screw eyes set on top of a smaller supporting disc that was fastened to a post (see photograph in Wilkinson 1964). Bolts were taken to the field on 31 August in Rep. 1 and on 10 September in Rep. 2.

In each replicate, 10 bolts were suspended on each of 2 randomly-selected turntables with thick- and thin-phloem bolts alternating in position around the circumference of a given table. Bolts were suspended by inserting the screw hook through the screw eye. On the average, a bolt's top was 8 cm below the underside of the plywood turntable disc, and the bottom of the bolt was 85 cm above groundline; neighboring bolts were 13-17 cm apart. Once suspended, the gelatin capsules were removed and the boring frass emptied into the bark crevice just below the starter hole. The bolts were then left to undergo natural infestation with the number of attacks on each bolt (as evidenced by boring frass) recorded after 48 and 96 h in the field.

Bolt mapping

After 10 days of exposure in the field, 4 thick- and 4 thin-phloem bolts were returned to the laboratory and frozen in both Reps. 1 and 2. This was done randomly by selecting 2 of the 5 bolts cut from each tree (2 bolts/tree x 8 trees = 16 bolts). These bolts were used as a record of spatial

attack, gallery construction, and reproduction. Bolts were returned to the laboratory on 10 and 20 September in Reps. 1 and 2, respectively.

An acetate map was made for each of the 16 bolts returned to the laboratory. Drawn first on each map were all major bark crevices. Then, following removal of the outer bark, all nuptial chambers, egg galleries, and egg niches of I. calligraphus (as well as all other associates) were drawn. Notes were added indicating egg hatch, extent of larval feeding, and any phloem discoloration. The two nuptial chambers on each bolt made by the artificially-introduced males were specially marked.

Installment of emergence traps on bolts

The remaining 24 bolts, 12 from each replicate, were kept in the field to allow for brood development and emergence. Four emergence traps were secured to each bolt when most individuals reached the pupal and callow adult stage (4 traps/bolt x 24 bolts = 96 traps). Pairs of traps were fastened on opposite sides of a bolt, centered 90° away from the starter holes. One of each pair of traps was placed on the upper half of the bolt and the other directly below on the lower half of the bolt, with about 5 cm separating their nearest edges. Traps were installed on 20 September in Rep. 1 and on 6 October in Rep. 2.

The traps were of simple design,[1] consisting of two 20x20 cm pieces of chipboard (1-ply), each with a 10x10 cm square removed from its center. A 30x30 cm section of nylon screen was folded and stapled to form a funnel. The wide end of the screen funnel was cut as needed, placed between the 2 chipboard sections and stapled so as to form a "sandwich" (the trap "base"). Staples were inserted end to end along the length of the funnel until only a space large enough to insert a 4-dram vial remained at the funnel's tip. A strip of Duxseal(R) was applied to the underside of the base along the inner perimeter. Later, traps were pressed to the bolt surface, the Duxseal(R) filling the bark crevices, and then stapled so that staples passed through both the base and Duxseal(R) before entering the bolt. A 4-dram vial was inserted part way into the funnel's tip and secured with a plastic-coated "twistem" wire. Vials were filled with 70% isopropyl alcohol, and so maintained throughout the study.

Data collection and analyses

Initial analyses. Initial analyses within each phloem thickness class indicated no significant ($P>0.05$) differences between Reps. 1 and 2 with respect to most of the parameters to be discussed below. The data were thus pooled in subsequent analyses.

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[1] The original trap design was developed by of Jeffrey A. Corneil, Oregon Department of Forestry, Route 2, Box 357, Prineville, Oregon 97754.

Spatial attack pattern. Analyses of the spatial attack pattern were facilitated by means of computer sampling. To avoid edge effects at the top and bottom of each bolt, only the central 50-cm-high band of each map was used in the analyses; by so doing the number of attacks used in the analyses decreased from 204 to 201. Each I. calligraphus nuptial chamber was considered an attack, with the entrance tunnel used as the "point" of attack. The position of each attack was given X and Y coordinates in millimeters on a per-bolt basis. The X and Y coordinates referred to positions along the bolt's circumference and height, respectively. These data were stored in a computer file. FORTRAN programs[2] were written so that each map was represented as a cylinder (i.e., as the original bolt), to afford sampling in both directions around the bolt's circumference.

The spatial attack pattern of I. calligraphus was analyzed by means of both quadrat and distance sampling (Pielou 1977). Morisita's (1959) index of dispersion, I-delta, represented the quadrat method. Distance sampling was employed using both "nearest neighbor" and "closest individual" techniques. The index "R" of Clark and Evans (1954), and as modified by Thompson (1956), represented the nearest neighbor and the nth nearest neighbor approaches, respectively. The closest individual technique was tested

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[2] FORTRAN programs were written by Jeffrey A. Corniel.

by means of Pielou's (1959) index of non-randomness, I-alpha. The index "A" of Hopkins and Skellam (1954) was the final method used; it involves aspects of both nearest neighbor and closest individual distance sampling. For each of the above tests, analyses were conducted within each phloem thickness class, and again for all data combined.

I-delta of Morisita. The Morisita index of dispersion is considered to be unaffected by mean density of the population being sampled (Morisita 1959), although this assumption may not always hold true (Taylor 1984). Morisita's index takes on the value of 1 and varies little with change in quadrat size when the distribution is random, it is >1 and either increases or decreases systematically with change in quadrat size when aggregated (clumped or contagious by other authors), and it is <1 and increases with increasing quadrat size when regular (uniform) (Morisita 1959). In the present study, each map was repeatedly sampled with quadrats ranging in size from 2x2 cm to 20x20 cm, with dimensions increasing in length by 2 cm on each successive pass.

The index R of Clark and Evans and of Thompson. To employ this nearest neighbor technique, a density estimate (D) and a sample of distances (r) from random individuals to their nearest and/or nth nearest neighbor are required. The index of non-randomness is R, and it is the ratio of the

observed to the expected mean distance in an infinitely large random distribution (Clark and Evans 1954). Therefore, R has an expected value of 1 when the distribution is random, <1 when aggregated, and >1 when regular. Significance of departure from randomness is tested using "c," the standard variate of the normal curve. Calculation of this statistic is presented for the (1st) nearest neighbor in Clark and Evans (1954) and for the 2nd to 4th nearest neighbors in Thompson (1956). The advantage of the Thompson method over the Clark and Evans test is that it allows for detection of larger scale heterogeneity than is possible by simply using distances to the 1st nearest neighbor (Thompson 1956). Distances to the 1st through the 4th nearest neighbor were calculated for all attacks (201 attacks X 4 distances/attack = 804 distances). Significance of departure from randomness was tested using c at the $P<0.05$ level. R values for thick and thin phloem were compared using the test provided in the appendix to Clark and Evans (1954).

Pielou's index of non-randomness, I-alpha. Pielou's index I-alpha requires both a sample of distances from randomly selected points to the closest individuals and an estimate of density. The index I-alpha assumes the value of 1 when the distribution is random, >1 when aggregated, and <1 when regular (Pielou 1959). For each map, 25 random points were generated and the distance to the closest

individual from each was calculated (25 points/map X 16 maps = 400 points). The I-alpha values were tested for non-randomness using the chi-square distribution as described by Pielou (1959).

The Hopkins and Skellam index A. The test of Hopkins and Skellam (1954) is based on the assumption that if a pattern is random, then the distribution of the distances from a random point to its closest individual is identical with the distribution of the distances from a random individual to its nearest neighbor. In this test, "P" is a point-to-individual distance and "I" is an individual-to-neighbor distance. The index "A" has an expected value of 1 if the pattern is random, >1 if aggregated, and <1 if regular. The statistic "X" is used to test for non-randomness using the tables of the normal curve probability integral (Pearson 1924). For each map, 10 points and 10 attacks were selected randomly, and the distance from each to the next closest attack was calculated (20 distances/map X 16 maps = 320 distances).

Attack density. Attack density was calculated for each of the 16 bolts (maps) as follows: Attack density (nuptial chambers/dm^2) = No. of Attacks/Bolt Surface Area (inside bark). The t-test was used to compare average attack density between thick and thin phloem on the basis of all nuptial chambers (NC), and for those that had 1 or more

associated egg galleries (ENC). In each nuptial chamber category, male presence was treated equally, i.e., all well-constructed nuptial chambers were considered in the analyses regardless if a male was present or not at the time of bolt dissection. Additionally, linear regression of both NC and ENC was performed with phloem thickness. These analyses and most of those that follow were performed using the t-test and general linear models procedures of the Statistical Analysis System (SAS), version 1982.3.

Harem size. The mating system of I. calligraphus is an example of "harem polygyny" (Kirkendall 1983), i.e., typically more than one female per male. The number of egg galleries starting from each nuptial chamber were counted. In general, a parent female was found within each gallery; thus, each egg gallery was considered to represent 1 female. The average number of egg galleries per nuptial chamber was compared between thick and thin phloem by means of the t-test; comparisons were made on both a NC- and ENC-basis. Additionally, the number of galleries per-NC and per-ENC were compared within each phloem thickness class between gallery systems initiated by artificially-introduced and wild males (t-test).

Gallery density. For each egg gallery, measurements were made on the length of initial egg-free gallery (PRE-EG, cm) starting from the junction with the nuptial chamber, egg-

bearing gallery (EG, cm), and terminal egg-free gallery (POST-EG, cm). Total gallery length (TG, cm) was calculated as the sum PRE-EG, EG, and POST-EG. The length of total egg-free gallery (EFG, cm) was the sum of PRE-EG and POST-EG. Density values for TG, EG, and EFG (each per-dm^2) were calculated on a per-bolt basis as described above. Average TG, EG, and EFG densities were each compared between thick and thin phloem using the t-test. Additionally, linear regression was performed on each of these density parameters with phloem thickness.

For the sake of discussion and comparison, TG, PRE-EG, EG, POST-EG, and EFG were (1) compared between phloem thickness classes on a per-gallery and per-nuptial chamber (both NC and ENC) basis, and (2) within each phloem thickness class, between gallery systems initiated by introduced and wild males on both a per-NC and per-ENC basis.

Egg density. The number of egg niches found in each gallery was recorded. Average egg density (eggs/dm^2) was calculated on a per-bolt basis as described above. Average egg density was compared between thick and thin phloem (t-test). In addition, regression analysis was performed on egg density with phloem thickness.

In order to make comparisons to the previously discussed laboratory studies, linear egg density (eggs/cm of gallery) was calculated for each gallery on a per-TG and per-EG

basis; these values were compared by means of the t-test. The percentage of each gallery that contained eggs was defined as: %EG = EG/TG x 100. Average %EG was compared between phloem thickness classes (t-test) after arcsin transformation as described in Steel and Torrie (1980).

Eggs per gallery and per nuptial chamber were calculated and compared between thick and thin phloem (t-test), with the latter comparison made on both a per-NC and per-ENC basis. Within each phloem thickness class, eggs/nuptial chamber were compared between galley systems initiated by introduced versus wild males (t-test).

Time to 50% brood emergence. Emergence traps were checked daily in late afternoon (1600-1800 h EST) for brood adults; catches were recorded by bolt and trap number. Adults that had not yet fallen into a vial were jostled with a pencil until so doing. Every 2-4 days the vials were emptied of their contents, put into place again, and refilled with alcohol. The collected brood adults were stored by tree number, i.e., 1 of the 8 trees originally felled. The average number of days to 50% brood emergence (for all adults collected in traps) was calculated for each phloem thickness class starting from the day the bolts were placed in the field. Average times to 50% emergence were compared between thick and thin phloem using the t-test.

Brood density. Brood density (No./dm²) values were based on the total number of brood adults collected on a per-trap basis. Means were compared between phloem thickness classes using the t-test. Regression was performed on brood density with phloem thickness.

Egg-to-adult mortality. Egg-to-adult brood mortality was approximated for each of the 16 dissected bolts using (1) the average egg density value for a given bolt, and (2) an estimate of final brood density for that same bolt. The brood density value assigned to a given bolt was the average of all trap (N=8) catches from 2 of the 3 bolts that had been cut from the same tree and matched most closely in phloem thickness. Means were compared between thick and thin phloem using the t-test after arcsin transformation of the data. Regression analysis of percent mortality was performed with phloem thickness without transformation.

Sex ratio. All brood adults collected in the emergence traps were sexed. The male proportion of all brood adults that emerged from thick and thin phloem were compared to 0.5 (the proportion expected in a 1:1 sex ratio) and to each other using the z-tests as described in Freund (1960, pp. 253 and 257).

Pronotal width. The pronotal width of 200 brood males and 200 females was measured using a microscope with micrometer. A total of 25 of each sex was chosen randomly

to represent each of the 8 trees from which bolts had been cut. Mean pronotal width was compared for males and females separately between thick and thin phloem using the t-test. In addition, pronotal widths of males and females were compared within each phloem thickness class (t-test). Linear regression analyses were performed on male and female pronotal widths (separately and combined) with phloem thickness.

Results

Spatial attack pattern. In general, the spatial attack pattern of I. calligraphus was regular both in thick and thin phloem. Specifically, the Morisita index values increased from 0 to near 1 with increasing quadrat size (Table 6-1), suggesting a regular pattern. The R values of the Clark and Evans test and the Thompson test were significantly ($P<0.01$) greater than 1 for both thick and thin phloem (Table 6-2), indicating a regular pattern for the 1st through the 4th nearest neighbor. The average distance between nearest neighbor (1st) attacks was about 9 cm. The Clark and Evans R values for thick and thin phloem were significantly different ($P<0.05$; $df=1,199$; $F=4.45$), indicating a more perfectly regular distribution (i.e., hexagonal) on thick phloem. Pielou's index of non-randomness indicated a significantly non-random (towards regular) spatial attack pattern on thick phloem ($P<0.01$),

but not on thin phloem nor when the two phloem thickness classes were combined ($P<0.05$) (Table 6-3). The Hopkin and Skellam index indicated a significantly ($P<0.05$) non-random (towards regular) spatial attack pattern on both thick and thin phloem (Table 6-3).

Attack density. A total of 204 nuptial chambers was found within the phloem on the 16 bolts that were exposed in the field for 10 days: 119 in the case of bolts with thick phloem, and 85 in the case of thin phloem bolts. Average NC/dm^2 and ENC/dm^2 did not differ significantly between phloem thickness classes (Table 6-4). Nevertheless, a significant positive correlation was found between NC/dm^2 and phloem thickness (Table 6-5). However, no significant regression was noted between ENC/dm^2 and phloem thickness ($P>0.15$)

Harem size. A total of 538 galleries was recorded from the 16 bolt maps: 314 on thick phloem and 224 on thin phloem. Harem size ranged from 0-6 females per male on both thick and thin phleom. Average number of galleries/NC did not differ significantly between phloem thickness classes (Table 6-6). However, on a per-ENC basis, significantly more females had joined males in thick compared to thin phloem, averaging 12% more (Table 6-7).

Considering each phloem thickness class separately, the number of females that joined introduced males did not

differ from the number joining wild males in either thick or thin phloem, on either a per-NC or per-ENC basis (Tables 6-8 to 6-11). Frequency distributions of the number of egg galleries per nuptial chamber are presented in Table 6-12 for several of the above categories. Most nuptial chambers that lacked egg galleries did however have an active male present; these nuptial chambers appeared to have been recently constructed. A few of the nuptial chambers that lacked egg galleries appeared to have been abandoned.

Gallery density. A total of 70.5 m of egg gallery was measured: 39.8 m on thick phloem and 30.7 m on thin phloem. The gallery density parameters TG/dm^2 and EFG/dm^2 did not differ significantly between thick and thin phloem. However, with respect to EG/dm^2, there was a weakly significant ($P<0.10$) difference between phloem thickness classes (Table 6-4). A significant linear relationship was found between EG/dm^2 and phloem thickness (Table 6-5); the two were positively correlated. However, no significant regression was calculated for either TG/dm^2 ($P>0.11$) or EFG/dm^2 ($P>0.84$).

On a per-NC basis, the length of TG, PRE-EG, and EG were similar ($P>0.05$) between phloem thickness classes, but more POST-EG and EFG were constructed in thin versus thick phloem (88 and 57% more, respectively; Table 6-6). On a per-ENC basis, similar results occurred except that more EG/ENC was constructed in thick versus thin phloem, averaging 12% greater (Table 6-7).

In general, gallery measurements on a per-NC or per-ENC basis were similar between gallery systems of introduced males and wild males on thick phloem (Tables 6-8 and 6-9). However, in thin phloem, gallery systems of introduced males had significantly more EG/ENC and POST-EG/ENC than did those of wild males; The difference between TG per-NC or per-ENC on thick and thin phloem was weakly significant ($P<0.10$) (Tables 6-10 and 6-11).

On an individual gallery basis, females constructed more length of total gallery (TG) in thin versus thick phloem, averaging 8% more in thin phloem. This did not result from differences in the egg-bearing portion (EG), but rather from longer initial egg-free gallery (PRE-EG, 15% more) and terminal egg-free gallery (POST-EG, 88% more) in thin phloem. Therefore, it logically follows that on the average, females in thin phloem constructed more total egg-free gallery (EFG, 55% more) (Table 6-13).

Egg density. A total of 23,994 egg niches was counted, 16,115 in thick phloem and 7,879 in thin phloem. Females laid significantly more eggs/dm^2 in thick versus thin phloem, averaging 91% more (Table 6-4). Egg density was positively correlated with phloem thickness; the linear regression model is given in Table 6-5.

With respect to the entire gallery system, more eggs were laid in thick versus thin phloem on both a per-NC and per-ENC basis (Tables 6-6 and 6-7). On thick phloem, gallery systems initiated by introduced males did not contain

significantly more eggs than those of wild males on either a per-NC or per-ENC basis (Tables 6-8 and 6-9). This was not the case in thin phloem, however, where more eggs were associated with gallery systems of introduced versus wild males (Tables 6-10 and 6-11).

With respect to individual galleries, females in thick phloem laid more eggs per-gallery (46% more), as well as more eggs per-cm of gallery (36% more for EG, 25% more for TG) than did females in thin phloem. Females in thick phloem filled a greater percent of their galleries with eggs than did females in thin phloem; %EG was 16% greater in thick phloem.

Time to 50% brood emergence. Overall, 1369 brood adults were collected from the 96 emergence traps: 1065 from thick phloem and 304 from thin phloem. Significantly fewer days were required to achieve 50% brood emergence on thick than on thin phloem, averaging about 3 days sooner on thick phloem (Table 6-14).

Brood density. Significantly more brood adults emerged per-dm^2 of bark on thick compared to thin phloem; brood density was nearly 200% greater on thick phloem (Table 6-14). The linear regression model of brood/dm^2 with phloem thickness is presented in Table 6-5; the two were positively correlated.

Egg-to-adult mortality. Egg-to-adult mortality was significantly higher in thin versus thick phloem, averaging 16% higher in thin phloem (Table 6-14). A significant negative correlation was found between egg-to-adult mortality and phloem thickness; the regression model is presented in Table 6-5.

Brood sex ratio. Overall, about 45% of the brood adults were male. The male proportions of brood adults that emerged from thick and thin phloem were similar (Table 6-14). Considering each phloem thickness class separately, the male proportion of brood adults was significantly ($P<0.05$) different from 0.5 for thick-phloem reared adults, but not for thin-phloem reared adults.

Body size. Brood adult body size, as measured by pronotal width, was greater for both males and females when development occurred in thick rather than thin phloem, averaging 8% wider for males and 5% wider for females (Table 6-14). For thick-phloem reared adults, male pronotal width was greater than that of females, averaging about 4% wider. However, when development occurred in thin phloem, the sexes were of similar size. Pronotal width was positively correlated with phloem thickness for both males and females separately, and for both sexes combined. Linear regression equations are presented in Table 6-5.

Table 6-1. The spatial attack pattern of Ips calligraphus on slash pine bolts with thick (3-4 mm, N=8) or thin (1-2 mm, N=8) phloem, as described by Morisita's (1959) index of dispersion I-delta with varying quadrat size. Bolts were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

Quadrat Dimensions (cm)	I-delta of Morisita[1]		
	Phloem Thickness Class		
	Thick	Thin	Combined
2 x 2	0.00	0.00	0.00
4 x 4	0.00	0.00	0.00
6 x 6	0.15	0.24	0.19
8 x 8	0.24	0.62	0.39
10 x 10	0.58	0.62	0.60
12 x 12	0.39	0.77	0.53
14 x 14	0.76	0.79	0.78
16 x 16	0.73	0.99	0.84
18 x 18	0.82	0.98	0.88
20 x 20	0.81	0.96	0.87

[1]I-delta has an expected value of 1 if the pattern is random, >1 if aggregated, and <1 if regular.

$$\text{I-delta} = q \sum_{i=1}^{n} n_i (n_i - 1)/[N(N-1)]$$

, where q=number of sampling units, n_i =number of individuals in the ith unit, and N=total number of individuals in the sample.

Table 6-2. The spatial attack pattern of *Ips calligraphus* on slash pine bolts with thick (3-4 mm, N=8) or thin (1-2 mm, N=8) phloem, as described by the Clark and Evans (1954) nearest (1st) neighbor and the Thompson (1956) nth (2nd-4th) nearest neighbor tests. Bolts were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

Parameters*	Phloem Thickness Class		
	Thick	Thin	Combined
Area (cm^2)	19,294	17,475	36,770
Attacks/cm^2=D	0.00612	0.00475	0.00547
No. of attacks=N	118	83	201
1st Nearest Neighbor			
SUM(r)	1070	772	1842
SUM(r^2)	10,502	8319	18,821
MEAN(r)	9.07	9.30	9.17
R	1.42	1.28	1.36
c	8.64	4.89	9.58
2nd Nearest Neighbor			
SUM(r)	1431	999	2430
SUM(r^2)	18,441	13,373	31,814
MEAN(r)	12.13	12.04	12.09
R	1.27	1.10	1.19
c	7.93	2.67	7.51
3rd Nearest Neighbor			
SUM(r)	1681	1254	2935
SUM(r^2)	25,289	20,278	45,507
MEAN(r)	14.24	15.11	14.60
R	1.19	1.11	1.15
c	6.95	3.43	7.32
4th Nearest Neighbor			
SUM(r)	1943	1473	3416
SUM(r^2)	33,447	28,163	61,610
MEAN(r)	16.47	17.74	16.99
R	1.18	1.12	1.15
c	7.63	4.23	8.32

*Parameter derivations are given in Clark and Evans (1954) and Thompson (1956). The index R has an expected value of 1 if the pattern is random, <1 if aggregated, and >1 if regular. All R values are significantly ($P<0.01$) different from random.
"c"=the standard variate of the normal curve and is used as an F-value to test R for non-randomness.
"r"=distance (cm) from one individual to nearest neighbor.

Table 6-3. The spatial attack pattern of Ips calligraphus on slash pine bolts with thick (3-4 mm, N=8) or thin (1-2 mm, N=8) phloem, as described by Pielou's (1959) index of non-randomness I-alpha, and the index A of Hopkins and Skellam (1954). Bolts were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

Parameters	Phloem Thickness Class		
	Thick	Thin	Combined
I-alpha of Pielou*			
MEAN(w), where $w=r^2$	37.96	75.23	56.59
Attacks/cm^2=D	0.00612	0.00475	0.00547
I-alpha =MEAN(w)xPixD	0.73	1.12	0.97
P<	0.05	n.s.	n.s.
No. of Samples (r's)	200	200	200
A of Hopkins and Skellam**			
SUM(P^2)	3260	5294	8554
SUM(I^2)	8459	9688	18,147
A = SUM(P^2)/SUM(I^2)	0.39	0.55	0.47
P<	0.01	0.01	0.01
No. of samples (P's,I's)	80,80	80,80	160,160

*The index I-alpha has an expected value of 1 if the pattern is random, >1 if aggregated, and <1 if regular. For each map (bolt), 25 random points were generated and the distance (r) to the closest individual was calculated.

**The index A has an expected value of 1 if the pattern is random, >1 if aggregated, and <1 if regular. For each map (bolt), 10 point-to-individual (P) distances and 10 individual-to-neighbor (I) distances were calculated.

Table 6-4. *Ips calligraphus* total nuptial chambers (NC), nuptial chambers with 1 or more egg galleries (ENC), total gallery length (TG, cm), egg-bearing gallery (EG, cm), total egg-free gallery (EFG, cm), and eggs per dm^2 of bark surface area for slash pine bolts with thick (3-4 mm) or thin (1-2 mm) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

Parameter	Thick Phloem $\bar{X} \pm SD$ (Range)	Thin Phloem $\bar{X} \pm SD$ (Range)	$p^1 <$
Bolts (N)	8	8	
Area dm^2	26.1 ± 3.2 (19.8 - 29.7)	24.1 ± 1.2 (22.4 - 26.4)	0.12
NC/dm^2	0.58 ± 0.14 (0.36 - 0.81)	0.44 ± 0.23 (0.24 - 0.69)	0.14
ENC/dm^2	0.46 ± 0.18 (0.25 - 0.75)	0.39 ± 0.17 (0.24 - 0.68)	0.46
TG cm/dm^2	19.4 ± 6.5 (12.5 - 29.0)	15.9 ± 7.9 (5.0 - 28.9)	0.34
EG cm/dm^2	15.1 ± 5.0 (9.9 - 23.3)	10.7 ± 4.8 (3.7 - 18.4)	0.10
EFG cm/dm^2	4.4 ± 2.0 (1.9 - 7.6)	5.2 ± 3.1 (1.3 - 10.4)	0.52
Eggs/dm^2	78.3 ± 29.2 (48 - 123)	40.9 ± 16.3 (17 - 64)	0.01

[1]Means were compared using the t-test.

Table 6-5. Equations, coefficients of determination (r^2), standard error (Sy.x), and the ANOVA significance level (P) for linear regression models pertaining to Ips calligraphus nuptial chamber density (NC, No./dm^2), egg-bearing gallery density (EG, mm/dm^2), egg density (eggs/dm^2), brood density (F1, No./dm^2), egg-to-adult mortality (%MORT, %), and pronotal width of brood adults (PW, mm), with phloem thickness (PT, mm). Data were obtained from a field study in which slash pine bolts with phloem ranging from 1-4 mm thick were exposed to natural attack during the period September-November 1982 near Gainesville, Florida.

N*	Equation	r^2	Sy.x	P<
16	NC = 0.337 + 0.077PT	0.25	0.035	0.05
16	EG = 70.13 + 25.99PT	0.35	9.46	0.02
16	ED = 13.81 + 20.25PT	0.65	3.95	0.01
96	F1 = -0.52 + 6.19PT	0.44	0.74	0.01
16	%MORT = 89.75 - 4.79PT	0.31	1.91	0.03
200	Male PW = 1.68 + 0.050PT	0.19	0.009	0.01
200	Female PW = 1.67 + 0.028PT	0.11	0.006	0.01
400	M + F PW = 1.68 + 0.038PT	0.13	0.005	0.01

*N=number of bolts for ED, EG, NC, and M; number of emergence traps for D; and number of brood adults measured for PW.

Table 6-6. *Ips calligraphus* galleries (Gals.), total gallery length (TG, cm), initial egg-free gallery (PRE-EG, cm), egg-bearing gallery (EG, cm), terminal egg-free gallery (POST-EG, cm), total egg-free gallery (EFG, cm), eggs per nuptial chamber (NC) in slash pine bolts with thick (3-4 mm, N=8) or thin (1-2 mm, N=8) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

Parameter	Thick Phloem $\bar{X} \pm$ SD (Range)	Thin Phloem $\bar{X} \pm$ SD (Range)	P[1]<
No. of NC	119	85	
Gals./NC	2.64 ± 1.71 (0 - 6)	2.64 ± 1.35 (0 - 6)	0.99
TG/NC	33.9 ± 24.7 (0 - 95.9)	36.2 ± 22.1 (0 - 86.5)	0.50
PRE-EG/NC	3.4 ± 2.5 (0 - 10.7)	4.0 ± 2.4 (0 - 9.7)	0.10
EG/NC	26.4 ± 20.3 (0 - 83.0)	24.3 ± 16.4 (0 - 71.3)	0.43
POST-EG/NC	4.2 ± 4.1 (0 - 18.4)	7.9 ± 6.0 (0 - 27.6)	0.01
EFG/NC	7.6 ± 6.1 (0 - 27.5)	11.9 ± 8.0 (0 - 34.4)	0.01
Eggs/NC	137.7 ± 105.3 (0 - 394)	92.7 ± 61.7 (0 - 253)	0.01

[1]Means were compared using the t-test.

Table 6-7. *Ips calligraphus* galleries (Gals.), total gallery length (TG, cm), initial egg-free gallery (PRE-EG, cm), egg-bearing gallery (EG, cm), terminal egg-free gallery (POST-EG, cm), total egg-free gallery (EFG, cm), eggs per nuptial chamber with 1 or more egg galleries (ENC) in slash pine bolts with thick (3-4 mm, N=8) or thin (1-2 mm, N=8) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

Parameter	Thick Phloem $\bar{X} \pm$ SD (Range)	Thin Phloem $\bar{X} \pm$ SD (Range)	P[1]<
No. of ENC	95	76	
Gals./ENC	3.31 ± 1.19 (1 - 6)	2.95 ± 1.06 (1 - 6)	0.04
TG/ENC	42.5 ± 19.9 (1.2 - 95.9)	40.5 ± 19.3 (2.3 - 86.5)	0.50
PRE-EG/ENC	4.3 ± 2.1 (0.6 - 10.7)	4.5 ± 2.1 (0.5 - 9.7)	0.54
EG/ENC	33.0 ± 17.2 (0.6 - 83.0)	27.2 ± 14.9 (1.6 - 71.3)	0.02
POST-EG/ENC	5.2 ± 3.9 (0 - 18.4)	8.8 ± 5.7 (0 - 27.6)	0.01
EFG/ENC	9.5 ± 5.3 (0.6 - 27.5)	13.3 ± 7.2 (0.7 - 34.4)	0.01
Eggs/ENC	172.4 ± 88.6 (4 - 394)	103.7 ± 54.9 (6 - 253)	0.01

[1]Means were compared using the t-test.

Table 6-8. *Ips calligraphus* galleries (Gals.), total gallery length (TG, cm), initial egg-free gallery (PRE-EG, cm), egg-bearing gallery (EG, cm), terminal egg-free gallery (POST-EG, cm), total egg-free gallery (EFG, cm), and eggs on a per nuptial chamber (NC) basis comparing between NC's initiated by introduced males versus wild males in slash pine bolts with thick (3-4 mm, N=8) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

	Performance in Thick Phloem		
	Introd. Male	Wild Male	
Parameter	$\bar{X} \pm$ SD (Range)	$\bar{X} \pm$ SD (Range)	$P^1 <$
No. of NC	16	103	
Gals./NC	2.69 ± 1.74 (0 - 5)	2.63 ± 1.71 (0 - 6)	0.91
TG/NC	41.8 ± 30.8 (0 - 96)	32.7 ± 23.5 (0 - 84)	0.18
PRE-EG/NC	4.5 ± 3.1 (0 - 8)	3.3 ± 2.4 (0 - 11)	0.08
EG/NC	32.4 ± 24.7 (0 - 83)	25.4 ± 19.5 (0 - 70)	0.20
POST-EG/NC	4.9 ± 5.8 (0 - 18)	4.1 ± 3.8 (0 - 18)	0.56
EFG/NC	9.4 ± 7.8 (0 - 25)	7.3 ± 5.8 (0 - 28)	0.21
Eggs/NC	170 ± 126 (0 - 388)	133 ± 101 (0 - 394)	0.19

[1]Means were compared using the t-test.

Table 6-9. *Ips calligraphus* galleries (Gals.), total gallery length (TG, cm), initial egg-free gallery (PRE-EG, cm), egg-bearing gallery (EG, cm), terminal egg-free gallery (POST-EG, cm), total egg-free gallery (EFG, cm), and eggs on a per egg-gallery containing nuptial chamber (ENC) basis comparing between ENC's initiated by introduced males versus wild males in slash pine bolts with thick (3-4 mm, N=8) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

	Performance in Thick Phloem		
	Introd. Male	Wild Male	
Parameter	$\bar{X} \pm SD$ (Range)	$\bar{X} \pm SD$ (Range)	$p^1 <$
No. of ENC	13	82	
Gals./ENC	3.31 ± 1.25 (1 - 5)	3.30 ± 1.19 (1 - 6)	0.99
TG/ENC	51.5 ± 25.5 (9 - 96)	41.1 ± 18.6 (1 - 84)	0.08
PRE-EG/ENC	5.5 ± 2.4 (1 - 8)	4.1 ± 2.0 (1 - 11)	0.03
EG/ENC	39.9 ± 20.9 (7 - 83)	31.9 ± 16.4 (1 - 70)	0.12
POST-EG/ENC	6.1 ± 5.8 (0 - 18)	5.1 ± 3.5 (0 - 18)	0.56
EFG/ENC	11.6 ± 6.7 (2 - 25)	9.2 ± 4.9 (1 - 28)	0.14
Eggs/ENC	209 ± 108 (43 - 388)	167 ± 85 (4 - 394)	0.11

[1]Means were compared using the t-test.

Table 6-10. *Ips calligraphus* galleries (Gals.), total gallery length (TG, cm), initial egg-free gallery (PRE-EG, cm), egg-bearing gallery (EG, cm), terminal egg-free gallery (POST-EG, cm), total egg-free gallery (EFG, cm), and eggs on a per nuptial chamber (NC) basis comparing between NC's initiated by introduced males versus wild males in slash pine bolts with thin (1-2 mm, N=8) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

	Performance in Thin Phloem		
	Introd. Male	Wild Male	
Parameter	$\bar{X} \pm SD$ (Range)	$\bar{X} \pm SD$ (Range)	$P^1 <$
No. of NC	16	69	
Gals./NC	2.81 ± 1.33 (0 - 5)	2.59 ± 1.36 (0 - 6)	0.57
TG/NC	45.6 ± 25.3 (0 - 87)	34.0 ± 20.9 (0 - 85)	0.06
PRE-EG/NC	4.5 ± 2.5 (0 - 9)	3.9 ± 2.4 (0 - 10)	0.38
EG/NC	35.0 ± 20.9 (0 - 71)	21.9 ± 14.2 (0 - 65)	0.03
POST-EG/NC	6.2 ± 3.7 (0 - 13)	8.3 ± 6.4 (0 - 28)	0.10
EFG/NC	10.7 ± 5.8 (0 - 18)	12.2 ± 8.4 (0 - 34)	0.51
Eggs/NC	140 ± 81 (0 - 253)	82 ± 50 (0 - 189)	0.02

[1]Means were compared using the t-test.

Table 6-11. *Ips calligraphus* galleries (Gals.), total gallery length (TG, cm), initial egg-free gallery (PRE-EG, cm), egg-bearing gallery (EG, cm), terminal egg-free gallery (POST-EG, cm), total egg-free gallery (EFG, cm), and eggs on a per egg-gallery containing nuptial chamber (ENC) basis comparing between ENC's initiated by introduced males versus wild males in slash pine bolts with thin (1-2 mm, N=8) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

	Performance in Thin Phloem		
	Introd. Male	Wild Male	
Parameter	$\bar{X} \pm$ SD (Range)	$\bar{X} \pm$ SD (Range)	$P^1 <$
No. of ENC	15	61	
Gals./ENC	3.00 ± 1.13 (1 - 5)	2.93 ± 1.05 (1 - 6)	0.83
TG/ENC	48.7 ± 23.0 (7 - 87)	38.5 ± 17.9 (2 - 85)	0.07
PRE-EG/ENC	4.8 ± 2.3 (1 - 9)	4.4 ± 2.0 (1 - 10)	0.53
EG/ENC	37.3 ± 19.4 (5 - 71)	24.7 ± 12.6 (2 - 65)	0.03
POST-EG/ENC	6.6 ± 3.4 (0 - 13)	9.3 ± 6.0 (0 - 28)	0.03
EFG/ENC	11.4 ± 5.2 (2 - 18)	13.7 ± 7.6 (1 - 34)	0.26
Eggs/ENC	150 ± 74 (25 - 253)	92 ± 43 (6 - 189)	0.02

[1]Means were compared using the t-test.

Table 6-12. Frequency distributions of Ips calligraphus egg galleries per nuptial chamber for slash pine bolts with thick (TK, 3-4 mm, N=8) or thin (TN, 1-2 mm, N=8) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida. Several categories are considered: (1) the combined data for both thick and thin phloem, and then, for each phloem thickness class separately: (2) the overall distribution, (3) the distribution considering only nuptial chambers with 1 or more egg galleries, (4) the distribution considering only nuptial chambers constructed by introduced males, and (5) similarly, for only those nuptial chambers constructed by wild males.

Category	Phloem	Number of Egg Galleries / Nuptial Chamber							Total
		0	1	2	3	4	5	6	
		No. %[1]	No. (%)	No. (%)	No. (%)	No. (%)	No. (%)	No. (%)	
1		33 (16)	16 (8)	29 (14)	61 (30)	47 (23)	15 (8)	3 (1)	204
2	TK	24 (20)	7 (6)	16 (13)	31 (26)	25 (21)	14 (12)	2 (2)	119
2	TN	9 (11)	9 (11)	13 (15)	30 (35)	22 (26)	1 (1)	1 (1)	85
3	TK	-	7 (7)	16 (17)	31 (33)	25 (26)	14 (15)	2 (2)	95
3	TN	-	9 (12)	13 (17)	30 (40)	22 (29)	1 (1)	1 (1)	76
4	TK	3 (19)	2 (13)	1 (6)	2 (13)	7 (44)	1 (6)	0 (0)	16
4	TN	1 (6)	2 (13)	2 (13)	6 (38)	4 (25)	1 (6)	0 (0)	16
5	TK	21 (20)	5 (5)	15 (15)	29 (28)	18 (17)	13 (13)	2 (2)	103
5	TN	8 (12)	7 (10)	11 (16)	24 (35)	18 (26)	0 (0)	1 (1)	69

Table 6-13. Ips calligraphus total gallery length (TG, cm), initial egg-free gallery (PRE-EG, cm), egg-bearing gallery (EG, cm), terminal egg-free gallery (POST-EG, cm), total egg-free gallery (EFG, cm), percent of total gallery with eggs (%EG, %), eggs per gallery, and eggs per cm of gallery on the basis of both EG and TG, in slash pine bolts with thick (3-4 mm, N=8) or thin (1-2 mm, N=8) phloem that were allowed to undergo natural infestation for 10 days during September 1982 near Gainesville, Florida.

Parameter	Thick Phloem $\bar{X} \pm$ SD (Range)	Thin Phloem $\bar{X} \pm$ SD (Range)	P[1]<
Galleries (N)	314	224	
TG	12.7 ± 4.8 (1.2 - 31.5)	13.7 ± 4.2 (2.3 - 40.0)	0.01
PRE-EG	1.3 ± 0.6 (0.0 - 6.0)	1.5 ± 0.6 (0.5 - 5.1)	0.01
EG	9.8 ± 4.6 (0.6 - 28.0)	9.2 ± 4.4 (0.5 - 37.5)	0.12
POST-EG	1.6 ± 1.7 (0.0 - 12.7)	3.0 ± 2.1 (0.0 - 14.0)	0.01
EFG	2.9 ± 1.9 (5.0 - 14.0)	4.5 ± 2.3 (5.0 - 15.6)	0.01
%EG[1]	75.8 ± 14.8 (13 - 98)	65.4 ± 17.3 (10 - 97)	0.01
Eggs/Gallery	51.3 ± 23.3 (4 - 137)	35.2 ± 16.7 (1 - 103)	0.01
Eggs/cm of EG	5.4 ± 1.4 (2.7 - 23.0)	3.9 ± 0.8 (0.4 - 6.1)	0.01
Eggs/cm of TG	4.1 ± 1.3 (0.7 - 18.2)	2.5 ± 0.9 (0.2 - 5.3)	0.01

[1]Means were compared using the t-test. Analyses on %EG were conducted on the data after arcsin transformation.

Table 6-14. *Ips calligraphus* average number of days to 50% brood emergence (days), brood density (No./dm²), egg-to-adult brood mortality (%), and sex ratio (% males) and pronotal width (mm) of brood adults from slash pine bolts with thick (3-4 mm) or thin (1-2 mm) phloem. Bolts were exposed to natural attack during the period September-November 1982 near Gainesville, Florida.

Parameter	Thick Phloem N[1]	Thick Phloem $\bar{X} \pm SD$ (Range)	Thin Phloem N	Thin Phloem $\bar{X} \pm SD$ (Range)	P[2]<
50% Emergence	1065	34.9 ± 4.8 (27 - 56)	304	38.1 ± 7.9 (27 - 59)	0.01
Brood Density	48	20.0 ± 10.3 (4 - 50)	48	6.8 ± 5.9 (2 - 85)	0.01
Mortality	8	72.9 ± 10.9 (57 - 82)	8	84.9 ± 4.9 (79 - 93)	0.02
Percent Males	1065	45.3	304	44.6	0.79
Pronotal Width[3]					
Males	100	1.86 ± 0.12a (1.6 - 2.1)	100	1.72 ± 0.09a (1.5 - 1.9)	0.01
Females	100	1.78 ± 0.09b (1.55 - 1.95)	100	1.70 ± 0.09a (1.5 - 1.9)	0.01

[1]N=total number of brood adults collected in emergence traps for 50% Emergence and Percent Males, the number of traps for Brood Density, the number of bolts for Mortality, and the number of randomly selected brood adults that were measured for Pronotal Width.

[2]The t-test was used to compare between means (within rows) for 50% Emergence, Brood Density, Mortality (after arcsin transformation), and pronotal width; the z-test was used to compare the male percentages as proportions.

[3]Means followed by the same letter (within columns) are not significantly different at the $P<0.05$ level (t-test).

Discussion

Spatial attack pattern. For the most part, the indices of non-randomness used in this study indicated that the I. calligraphus attack pattern was regular. These results (at least in the case of thick phloem) are similar to those of a another study conducted in Florida, where J. A. Corneil (unpublished data) determined that I. calligraphus attacked in a regular pattern (using the Clark and Evans method) based on whole-tree analyses of 15 naturally infested slash pine trees; phloem thickness near breast height averaged 1.7 mm and ranged between 0.9-2.6 mm for these 15 trees. He recorded a mean attack density of 0.00646 attacks/cm^2 with an average nearest neighbor distance of 8.2 cm. Thus, because of the above similarities in both attack pattern and density, it is probable that the findings of this study are comparable to that which occurs in naturally attacked trees. The spatial attack patterns of several other bark beetle species have also been found to be regular (Shepherd 1965; Hedden and Gara 1976; Nilssen 1978).

Why would individuals distribute themselves regularly? Iwao (1970) reasoned that a regular distribution results when either (1) the habitat available for colonization is distributed regularly or (2) the individuals are competing with one another for a resource. Both of these hypotheses have appeared in the bark beetle literature. With respect to the first hypothesis, the regular distribution of bark

crevices was considered the principal factor leading to regular spacing in Dendroctonus ponderosae Hopkins (Shepherd 1965; Safranyik and Vithayasai 1971). In support of the second hypothsis are papers discussing competition by means of sonic signals and short-range repellent pheromones (Rudinsky 1969; Rudinsky and Michael 1972, 1973; Furniss et al. 1974).

Do the above factors influence spacing in I. calligraphus? In this study, males attacked mostly in bark crevices; about 93% of the nuptial chambers were entered via bark crevices and only 7% entered through major bark plates. Utilization of bark crevices would apparently be advantageous by providing (1) protection from predators, wind, and rain; (2) material to brace against when first entering the tree; (3) a shorter distance to tunnel before reaching phloem; and (4) a catch area for the pheromone-laden male frass. Nevertheless, the distribution of bark crevices does not appear to be the most important factor affecting the distribution of male attacks on slash pine. A line drawn around the circumference, at the middle of each of the 16 bolts from which maps were made, intersected an average of 2.6 bark crevices per linear dm (N=16; SD=0.30; range 2.0-3.2), indicating that colonization sites are abundant compared to the number of attacks found in a given area.

Ips calligraphus males are capable of producing "clicking" sounds (Wilkinson et al. 1967), but the possible function of such sound production has not been investigated. Rudinsky and Michael (1973) recorded "clicking" sounds made by females (the colonizing sex) of two Dendroctonus species and suggested that these sounds or other "chirping" sounds had an intraspecific spacing function when attacking females were selecting sites for the initiation of their galleries. Thus, another possible advantage to attacking in bark crevices is that sonic signals produced by resident beetles would be more readily sensed by later-arriving I. calligraphus males when walking in crevices rather than on the thick outer-bark plates. Sonic signals could pass through wood and bark equidistantly and may be an important spacing mechanism; Rudinsky and Michael (1973) discuss this hypothesis. Research is needed to determine if I. calligraphus males produce clicking sounds when in their nuptial chambers and the behavioral response of other males to these sounds.

Certain compounds in I. calligraphus male frass serve as aggregation pheromones to both sexes (Renwick and Vite 1972; Vite et al. 1972). It is possible that Ips pheromones serve to attract males when in low concentrations, as would occur when field populations fly to a tree that is under attack. However, once at the tree, these same pheromones may serve to repel males because of their then perceived higher

concentrations. This conjecture finds support in the fact that multiple functions for a single pheromone have been recorded for two Dendroctonus species (Rudinsky 1973a, 1973b). In the laboratory studies described in chapter III, I observed adult females to walk to a pile of male-produced frass (without males present) and burrow in it vigorously, and males to turn away when within about 5-10 cm of such piles. Such observations suggest that in the field, late-arriving males could utilize frass volatiles of resident males to space themselves so as to minimize intraspecific competition. It is quite possible that I. calligraphus males use a sequential combination of pheromones, bark topography, and sonic signals when spacing themselves on a given host.

Attack density. The fact that a direct positive relationship was found between attack density and phloem thickness (Table 6-5) indicates that aggregation may be regulated in part by pheromone "quality." Vite et al. (1972) reported that I. calligraphus males produced quantitatively less pheromone when in host materials with thinner phloem. Similarly, pheromone production by Ips paraconfusus was found to be directly related to phloem quality (Pitman 1966). Thus, I. calligraphus attack density may reflect the nutritional quality of the host, and thus serve as a feedback mechanism to avoid overpopulation of a nutritionally poor resource. It is of interest to note that

in the case of I. avulsus, a species cross-attracted to I. calligraphus pheromones (Renwick and Vite 1972), 14 of the 19 I. avulsus attacks were on thick-phloem bolts. Such observations suggest that pheromones and/or host volatiles may serve to adjust the numbers of beetles arriving at a host, and that a more definitive study should be conducted to test this hypothesis. Possibly the differences noted between thick and thin phloem would have been greater had the bolts been segregated by phloem thickness class on the turntables instead of mixed as was the case.

In light of the above discussion, it would seem probable that if spacing was regulated by a pheromone concentration gradient alone, then the presumably more potent pheromone "bouquet" produced on thicker phloem would result in wider spacing by males attacking thick-phloem trees. However this was not the case; mean nearest neighbor distances were 9.1 cm on thick phloem and 9.3 cm on thin phloem (Table 6-2). Such results suggest that sonic signals, if found to be made by I. calligraphus males in nature, may be the principal factor regulating spacing. Use of sonic signals for spacing would apparently be a more foolproof method since pheromone gradients would be easily altered by air movement; for further discussion see Rudinsky and Michael (1973). For purposes of discussion, if spacing is considered to be controlled primarily by sonic signals, then the slightly wider spacing of attacks on thin phloem may reflect the

denser nature of the wood, i.e., thinner phloem slash pines generally have narrower and denser annual rings of xylem (unpublished data) and thus may carry sound waves farther. Also, nuptial chambers would be constructed deeper in the xylem on thin phloem and thus may affect the sound wave produced; nuptial chambers could be considered "resonating" chambers. Whatever the mechanism, it is apparent that incoming I. calligraphus males attempt to space themselves relative to resident males so as to enhance their own reproductive success (Alcock 1981), i.e., to locate where food will be available for their progeny.

Harem size. Both in this study and the one reported by Cook et al. (1983), the situation of 3 females per male (3 galleries/nuptial chamber) was the most commonly found. How might this occur? Vite et al. (1972) reported that I. calligraphus males soon ceased to produce ipsdienol, an aggregation pheromone, when joined by 3 or more females. They also reported that ipsdienol production declined as the males aged. Reduced pheromone production by mated beetles has been demonstrated for I. paraconfusus males (Borden 1967) and Scolytus multistriatus (Marsh.) (Elliott et al. 1975). Nevertheless, the reasons for this phenomenon are not understood, but may include (1) hormonal changes that occur as a result of mating or aging, (2) a lack of substrate from which to produce pheromones given that males spend less time feeding (tunneling) once females are

present, and/or (3) a response to changing host conditions resulting from colonization by Ceratocystis ips and other microorganisms. Changes in phloem carbohydrates and amino acids as a result of Ceratocystis colonization have been documented by Hodges et al. (1968) and Barras and Hodges (1969).

Certain behavioral aspects of consorting I. calligraphus males and females may also limit harem size. Gouger et al. (1975) reported that males deposit their gelatinous feces on the nuptial chamber walls, and that consorting females consume the male's feces. Thus, it seems plausible that as the number of females in a given nuptial chamber increases, the amount of male-produced, pheromone-laden feces would diminish, and that this in itself could control harem size.

The fact that on thicker phloem more females were found on a per-ENC basis (Table 6-7) suggests that pheromone production (quantity and/or quality) and thus attractiveness to females, was greater. Apparently this is another instance where host quality regulates beetle density, in that harem size may be a function of pheromone production, with the latter being dependent on host quality.

Gallery density. Why is length of egg gallery per unit area positively correlated with phloem thickness? The 3 principal reasons are (1) that nuptial chamber density increased directly with phloem thickness (Table 6-5), (2) that more females joined each male (at least on a per-ENC

basis, Table 6-7), and (3) that a greater percent of each gallery contained eggs (%EG, Table 6-13).

Egg density. As was described in detail in chapter II, there are distinct nutritional and physical differences between phloem, xylem, and outer bark in pines. It was reported in chapters II and III that eggs/cm of gallery increased directly with phloem thickness, and an explanation for this phenomenon was put forth in terms of the above host tissue differences. In the present field study, linear egg density again was greater on thicker phloem (Table 6-13). In addition, eggs/dm^2 increased with increasing phloem thickness. Again, this probably reflects greater attack density, females/ENC, and %EG in thicker phloem as described in the above section, as well as greater egg density within each gallery.

Why is there more terminal egg-free gallery (POST-EG) in thin phloem? Many factors are likely involved in cessation of oviposition by bark beetles. The presumed nutritional and physical constraints to boring in thin phloem could cause parent females to change from a reproductive to a flying condition earlier in thin than in thick phloem. Dendroctonus ponderosae changes from a reproductive mode to a flying mode in response to declining phloem water content (Reid 1962).

Another possible factor is the interaction of parent females with feeding larvae (and/or their associated fungi,

yeast, and bacteria) from other gallery systems. As was mentioned in chapter IV, and again observed in the present study, larvae and phloem discoloration in thin phloem extended farther from the "mother" gallery for a given span of time than occurred in thick phloem. The microorganisms associated with a particular bark beetle species generally advance ahead (Leach et al. 1934; Farmer 1965), or lag slightly behind the feeding larvae (Whitney 1971). Ips calligraphus oviposition is almost completely inhibited in areas stained by its associated fungus, Ceratocystis ips (Yearian et al. 1972). Dendroctonus frontalis females also avoid egg laying in areas stained by their associated fungus, Ceratocystis minor (Franklin 1970). Such behavior would be adaptive in restricting oviposition to areas that are "sensed" to be unoccupied, and thus serve in regulating eventual brood density per unit of phloem as was suggested by Yearian et al. (1972). Therefore, assuming that (1) nuptial chamber spacing, (2) rate of colonization by males and females, (3) tunneling rates by ovipositing females (see chapters II and III), and (4) time to egg hatch are similar on both thick and thin phloem, then the fact that larvae tunnel faster in thinner phloem would allow for an earlier encounter between parent females and larvae of other broods and their symbionts in thin versus thick phloem. As a result, females in thinner phloem would probably cease oviposition sooner, and thus begin construction of the

terminal egg-free portion of the gallery at an earlier time relative to females in thicker phloem. This scenario could explain why POST-EG was longer in thinner phloem given that females construct more gallery per unit time once oviposition has ceased.

In thin phloem, gallery systems of introduced males contained more egg-bearing gallery and more eggs than did those of wild males. This did not occur in thick phloem. Such differences cannot be explained on the basis of differential rate of attack, rate of female arrival, nor number of females per attacking male. Regardless of phloem thickness, similar numbers of attacks/bolt were present after the second and fourth day of exposure in the field, as well as similar total gallery length and number of galleries per nuptial chamber after 10 days in the field. Thus, females probably arrived on thick and thin phloem bolts at about equal times. However, as discussed above, larval movement away from the "mother" gallery was more rapid in thinner phloem. Therefore, larvae that were fathered by introduced males would be more likely to inhibit oviposition of females in neighboring gallery systems earlier on thinner phloem. This would result in earlier cessation of oviposition by females joining wild males in thin compared to thick phloem. Such a scenario could explain why introduced males were more reproductively successful (i.e., fathered more progeny) than wild males on thin but not thick

phloem. Apparently in the case of I. calligraphus, given that a host is "safe" to colonize, there is greater advantage to being an initial colonizer when the available substrate is nutrient-poor rather than nutrient-rich.

Considering the foregoing discussion, there appear to be several "steps" at which host quality influences the number of eggs laid per unit area of phloem: (1) host quality may affect pheromone production and thus limit attack density, (2) similarly, the number of females joining any given male may be a function of pheromone production, (3) host quality affects the number of eggs laid per cm of gallery, and (4) the rate at which larvae tunnel may limit the egg-bearing length of gallery of females in neighboring gallery systems. Each of the above could lead to a reduction in final egg density, which in thin phloem would lead to lower larval competition for the limited food (phloem) resource. Thus, an intricate series of feedback loops seem to exist whereby the number of eggs laid in a given area is closely attuned with what the area can support.

Time to 50% brood emergence. The delayed brood emergence recorded from thin phloem in this field study supports the laboratory findings reported in chapter IV (Table 4-4). In that chapter, delayed emergence from thin phloem was discussed in terms of protracted development resulting from the presumed physical and nutritional constraints to tunneling in thinner phloem.

Brood density. Again, with respect to brood density, a laboratory finding was confirmed in the field. In laboratory studies (see Table 4-3), more progeny per parent female were produced in thicker phloem. In the present study, more progeny per unit area emerged in thicker phloem. The two principal factors that probably lead to greater brood density on thicker phloem were greater initial oviposition and lower egg-to-adult mortality.

Egg-to-adult mortality. Although few mortality data are available from laboratory studies, the existing information does not follow the trend recorded in the field. Mortality in the laboratory (see Discussion in chapter IV) generally ranged between 35-50% in both thick and thin phloem; such values are much lower than those reported in this field study. Possibly, the relatively low density of parent adults used (2 males and 6 females/bolt) in the laboratory studies, reduced the level of intraspecific competition compared to the field.

The egg and brood-adult density values obtained in this study are greater than those found in another field study involving 10 naturally infested slash pine trees in Florida. In that study, mean egg and brood adult densities for I. calligraphus were 36.7 egg/dm² (range 0-181) and 3.2 adults/dm² (range 0-25) (John L. Foltz[3] and Jeffrey A.

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[3] Department of Entomology and Nematology, University of Florida, Gainesville, Florida 32611.

Corneil, unpublished data). Egg-to-adult mortality based on these two values would be ca. 87%. Thus, the bolt values probably reflect development under relatively ideal conditions and limited intra- and interspecific competition.

Sex ratio. Brood adult sex ratios from thick and thin phloem were similar in this field study, but not in the laboratory study discussed in chapter IV (Table 4-9), where a 1:2 sex ratio (males:females) was reported for thin-phloem reared brood adults. Reasons for a female-biased sex ratio were discussed in chapter IV, with the main argument being that as a result of the presumably longer male developmental time, males are more prone to cannibalism and/or more adversely affected by the "harsh" conditions of thin phloem than were the faster developing females. If true, then the slightly "thicker" nature of the thin phloem used in the present field study (1-2 mm vs 0.5-1.5 mm) may have afforded the males a less severe environment under which to develop; see discussion and references noted in chapter IV.

Body size. The laboratory finding that both males and females were larger when reared from thicker phloem (Table 4-8) was confirmed in the present field study. Also, it was demonstrated in both lab and field studies that males were larger than females when reared in thick but not thin phloem. Plausible explanations for these results are discussed in chapter IV.

Summary

In summary, the following points can be made with respect to I. calligraphus attack, reproduction, and development under experimental field conditions.

1. The distribution of I. calligraphus nuptial chambers was regular on both thick and thin phloem according to the methods of Morisita, Clark and Evans, Thompson, and Hopkins and Skellam. The test of Pielou indicated a regular pattern on thick phloem only.
2. Attack density (nuptial chambers/dm^2) tended to increase with increasing phloem thickness.
3. The number of parent females per attacking male (egg galleries/nuptial chamber) ranged from 0 to 6 on both thick and thin phloem. Most commonly, the situation of 3 females per male is found. On the average, males on thick phloem are joined by more females than are males on thin phloem.
4. The length of egg-bearing gallery/dm^2 is positively correlated with phloem thickness.
5. Egg density (eggs/dm^2 and eggs/cm of gallery) increases with increasing phloem thickness (thus confirming earlier laboratory findings).
6. Average number of days to 50% brood adult emergence is significantly less on thicker phloem (thus confirming earlier laboratory findings).

7. Brood density (emerged F1 brood adults/dm^2) is positively correlated with phloem thickness. This finding supports laboratory observations in which F1 brood adults/parent female was greater in thicker phloem.
8. Egg-to-adult brood mortality is negatively correlated with phloem thickness. This finding is in contrast to laboratory results where mortality was less than that observed in the field, and similar between phloem thickness classes. The laboratory parent-adult stocking densities are discussed regarding this result.
9. The sex ratios of brood adults reared from thick and thin phloem in the field were similar; each was about 45% males. This finding is in contrast to laboratory results where 33% of the brood reared from thin phloem was male. The range of phloem thicknesses used in the two studies is discussed with respect to this result.
10. The pronotal widths of male and female brood adults are positively correlated with phloem thickness. Male pronotal width is greater than that of females when reared in thick but not thin phloem. These findings under field conditions confirm results from laboratory studies.

CHAPTER VII
CONCLUSIONS

The following conclusions and recommendations are made based on the results of the foregoing studies.

1. Both temperature and slash pine phloem thickness are important factors in the population dynamics of *I. calligraphus*, affecting aspects of beetle attack, reproduction, and development.
2. Specifically, significant relationships are found between both temperature and phloem thickness in their effects on (1) oviposition rate, (2) number of eggs laid per cm of gallery, (3) brood developmental rate, (4) average number of days to 50% brood adult emergence, (5) and brood production per parent female.
3. Temperature, more so than phloem thickness, is the principal factor affecting (1) rate of gallery construction, (2) length of initial egg-free gallery, and (3) average number of days to 50% parent adult re-emergence.
4. Phloem thickness is significantly correlated with (1) attack density (nuptial chambers/dm^2), (2) depth of xylem etching by females during gallery construction,

(3) cm of egg-bearing gallery/dm^2, (4) eggs/dm^2, (5) female longevity, (6) fecundity, (7) egg-to-adult brood mortality, (8) brood adult pronotal width, and (9) brood adult sex ratio.

5. Many of the laboratory findings with respect to phloem thickness effects were confirmed under experimental field conditions indicating that phloem thickness is a biologically relevant factor in the dynamics of I. calligraphus.
6. These results indicate that (1) great care should be taken when selecting host materials for bark beetle studies, especially when phloem thickness ranges from thinner to thicker than the average pronotal width of the females used in a study, (2) researchers should select experimental host materials that are representative of the trees typically found throughout their region, and (3) phloem thickness should be considered in biological studies of other phloem-inhabiting Buprestidae, Cerambycidae, and Curculionidae.
7. Phloem thickness should be considered in population dynamics studies of I. calligraphus in the slash pine ecosystem, especially in summer when warmer temperatures accentuate phloem thickness effects on reproduction and development of this bark beetle.

8. Future research should be directed at (1) partitioning the nutritional and physical aspects of lower performance in thinner phloem by means of artificial diets in which equal amounts of phloem from both thick- and thin-phloem slash pines are incorporated; (2) describing more fully the nutritional and physical characteristics of phloem, xylem, and outer bark in thick- and thin-phloem slash pines; and (3) obtaining more basic knowledge about the beetles themselves.

9. Specifically, basic research is needed to determine (1) if (1) if I. calligraphus males produce sound when within their nuptial chambers; (2) if and how pheromones, sound, and bark topography influence spatial distribution of attacking males; (3) how harem size is regulated; (4) the influencing factors leading to cessation of oviposition; (5) how male re-emergence is regulated; (6) if female size influences reproduction; (7) if male developmental time is longer than that of females; (8) the threshold temperature for I. calligraphus flight and oviposition; and (9) the factors influencing seasonal fluctuations in brood density.

10. An eventual outcome of this type of research could be a contribution to the development of pest management guidelines and a stand risk-rating system for I.

calligraphus in slash pine plantations. However, additional studies are needed to (1) develop phloem-thickness frequency distributions for slash pine plantations of varying age and site index, and (2) record the severity of *I. calligraphus* outbreaks in relation to average stand phloem thickness and other site and stand variables.

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BIOGRAPHICAL SKETCH

Robert Allen Haack was born in Madison, Wisconsin, on April 28, 1952. He graduated with honors from the University of Wisconsin-Madison in 1974 and 1975 after completion of B.Sc. programs in forest science and secondary science education, respectively.

Robert served as a U.S. Peace Corps volunteer in Guatemala, Central America, from 1975 to 1977, working primarily in the areas of soil conservation and forestry. He worked in Guatemala for an additional year as a regional director for CARE in the project entitled "Highlands Soil and Forest Conservation Program."

Robert completed his M.Sc. degree in entomology from the University of Wisconsin-Madison in 1980. He was awarded the 1980 Graduate Student Research Award by the Entomological Society of America-North Central Branch. Robert began his studies at the University of Florida in 1980 and is presently a candidate for the Doctor of Philosophy degree in entomology and nematology with a minor in plant pathology. He was awarded the Florida Entomological Society Scholarship Award in 1982.

The author has recently accepted a post-doctoral position at Michigan State University with the Department of Entomology.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Robert C. Wilkinson, Jr., Chairman
Professor of Entomology &
Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

George M. Blakeslee, Jr.
Associate Professor of Forest
Resources and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John L. Foltz
Associate Professor of Entomology &
Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank Slansky, Jr.
Assistant Professor of Entomology &
Nematology

This dissertation was submitted to the Graduate Faculty of the College of College of Agriculture and to the Graduate School, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

April 1984

Jack L. Fry
Dean, College of Agriculture

Dean for Graduate Studies and Research

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